Aspects of floral structure and development, and systematics in Laurales (Magnoliidae)

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To my family, to my friends

To my masters

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PREFACE

It is a long path from the childshood's dreams to the toil of adulthood, and it is a beautifull and rare thing to be able to keep ones child fascinations and make them to a profession. Biology is the science of the XXIst century, generating large fluxes of capital, and ever more refined tools. The pleasure to speculate has almost wanished, as the biologist became an engineer, rated as such, on his efficiency at using his ever more refined tools, and at setting up and trouble-shooting parallel experiments. The tremendous growth in available knowledge in the modern era has led to increased specialisations, which decrease overview. This lack of large perspective is not a problem for many scientists, but it is one for me. A scientist is a man that works a lot, and gets little pay, he therefore should choose his field with extreme care, as an improper choice may yield the frustration that is much more common in labs than is usually admitted. And this is why I chose to study evolutionary biology. A field linked to philosophy, chemistry and every day life, in which speculations are allowed, provided there is some support for them. I chose to work with flowers because I grew up surrounded by them, in a family of horticulturists.

GENERAL INTRODUCTION

Why study basal angiosperms ?

In the phylogenetic tree of the flowering plants (angiosperms) most groups are in two large clades, the Monocotyledoneae and the Eudicotyledoneae. A small group (ca. 3% of all angiosperm species) is distributed to several small relict clades, commonly know as "basal angiosperms". The largest clade of the basal angiosperms are the Magnoliidae (sensu Cantino et al. 2007) comprising two clades, the Magnoliales-Laurales clade and the Canellales-Piperales clade (Moore et al. 2007; Soltis et al. 2007). In basal angiosperms, there is a high variability in basic features of floral structure, such as merism, and phyllotaxis, which tend to be fixed in more derived groups, the Monocotyledoneae and Eudicotyledoneae. In these groups variability tends be at other structural levels based on synorganization of floral organs and even synorganization between flowers. It is reasonable to assume that the basal angiosperms have retained ancestral character states, so that their study allows better understanding of some key factors in the evolution of the more derived groups. Information on the basal angiosperms is also crucial for our understanding and interpretation of the fossil record, which despite its proverbial incompleteness, is our only direct testimony of macroevolution.

Why study Laurales ?

Laurales appear to show a high variability in floral structure (Perkins 1925; Kubitzki 1969; Schodde 1969; Endress 1980b; Rohwer 1993; Endress and Igersheim 1997; Renner and Hausner 2005), however, few comparative studies on the diversity of floral structure of this group have been undertaken to date. The presence of flowers with whorled and spiral phyllotaxis makes Laurales an appropriate study group for floral phyllotaxis variability and its association with other floral traits.

Gynoecium features in Laurales vary in some respects and are relatively constant in others. Hernandiaceae and Lauraceae have one carpel per flower, whereas the rest of the Laurales have pluricarpellate flowers. The carpels are almost always free and have superior ovaries (inferior and fused only in Gomortegaceae and *Tambourissa* of Monimiaceae). There is one, median, ovule per carpel in all Laurales, except in Calycanthaceae, which have two lateral ovules. Nevertheless, all Laurales produce one seed per carpel, and the fruits are indehiscent. Especially interesting is the gynoecium structure of Calycanthaceae, sister to the rest of the order, as it differs from all other families of the order.

Phylogenetic relationships within Laurales

Laurales comprise seven families and a few thousand extant species and still dominate some vegetations (e.g., laurel forests). Calycanthaceae (9 species; Zhou et al. 2006) are sister to the rest of the order, the core Laurales (Renner 1998, 1999, 2004; Qiu et al. 1999, 2005). The core Laurales consist of two subclades of three families each (Renner 2004): the clade containing Siparunaceae (53 spp.; Renner and Haussner 2005), Atherospermataceae (16 spp.; Renner et al. 2000), and Gomortegaceae (1 sp.; Kubitzki 1993), and the clade containing Monimiaceae (ca. 270 spp.; Philipson 1993), Hernandiaceae (ca. 60 spp.; Kubitzki 1969), and Lauraceae (2500-3500 spp.; Rohwer 1993). Siparunaceae are sister to Atherospermataceae plus Gomortegaceae (Renner 2004). Monimiaceae have an unsettled position either as sister to Lauraceae (Renner 1999, 2004), as sister to Hernandiaceae (Qiu et al. 1999, 2006), as sister to a clade comprising Hernandiaceae and Lauraceae (Doyle and Endress 2000; Chanderbali et al. 2001; Hilu et al. 2003), or the position of Hernandiaceae, Lauraceae and Monimiaceae is unresolved (Renner and Chanderbali 2000; Soltis et al. 2007).

Floral structure in Laurales

Floral phyllotaxis

Although Laurales appear to have unusual diversity in floral phyllotaxis, only few taxa have been studied in detail to date. In Calycanthaceae, the only studied species are *Calycanthus floridus* (Calycanthaceae) (Erbar and Leins 1983) and *Chimonanthus praecox* (Calycanthaceae, only perianth studied, Nelson 1954), which both show spiral phyllotaxis. In the pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, and Monimiaceae) it is poorly documented in detail, especially for the androecium and even more so the gynoecium. Descriptions of the floral phyllotaxis of the sole species of Gomortegaceae, *Gomortega keule*, show conflicting results (summarized in Kubitzki 1993). Atherospermataceae appear to be diverse, even at the genus level (Schodde 1969). The only documented species of Siparunaceae, *Siparuna thecaphora*, has decussate phyllotaxis in most male flowers and spiral in carpels of female flowers (Endress 1980a), but it may also be irregular in other taxa of the family (Renner and Hausner 2005). In Monimioideae of Monimiaceae, floral phyllotaxis is not known in detail. In Mollinedioideae of Monimiaceae, floral phyllotaxis is documented for whole flowers only in very few taxa: *Hortonia*, sister to the rest of the Mollinedioideae has a Fibonacci spiral phyllotaxis (Endress, 1980a). For most species studied, data are limited to the perianth, which is often decussate (Philipson 1993). Thus from the literature, floral phyllotaxis in Atherospermataceae and Monimiaceae appears unusually diverse and unstable. In contrast, in unicarpellate Laurales (Hernandiaceae and Lauraceae), floral phyllotaxis appears to be uniformly whorled (Kubitzki 1969; Hyland 1989; Endress and Lorence 2004).

Floral cup

A floral cup is present in almost all Laurales (Perkins 1925; Nicely 1965; Kubitzki 1969; Schodde 1969; Philipson 1993; Rohwer 1993; Renner and Haussner 2005), with the exception of some Lauraceae (Rohwer 1993). In some Monimiaceae, the floral cup encloses the reproductive organs almost completely (Siparunaceae, Monimiaceae). In some species of Monimiaceae, a hyperstigma, a receptive area for pollen outside the gynoecium, on the narrow floral pore formed by the floral cup and the reduced tepals is present (Endress 1980b).

Androecium

In Calycanthaceae, stamens are extrorse and have two thecae; they dehisce via longitudinal slits in extant taxa, and via laterally hinged valves in the fossils *Virginianthus* (Friis et al. 1994), and *Jerseyanthus*, (Crepet et al. 2005). In *Calycanthus* the tip of the connective is differentiated in protein-rich food bodies consumed by pollinating beetles (Rickson 1979), and such a differentiation also appears to be present on the ramified connective tips of the fossil *Jerseyanthus* (Crepet et al. 2005). In core Laurales, stamens are extrorse or introrse, have 2 or 4 thecae, dehisce via flaps in all families except Monimiaceae, and often bear two lateral glands (nectarines) on the filament (Gomortegaceae, Atherospermataceae, *Hortonia* and *Peumus* of Monimiaceae, Hernandiaceae and Lauraceae).

Inner staminodes are sterile stamen-like organs between stamens and carpels in bisexual flowers and occur in several families of basal angiosperms (Endress 1984). In all Calycanthaceae inner staminodes are present (Nicely 1965, also in fossils, Friis et al. 1994; Crepet et al. 2005). Among core Laurales, inner staminodes (often nectariferous) are present in *Gomortega* (Kubitzki 1993), Atherospermataceae (Schodde 1969), and in *Hortonia* of Mollinedioideae (Endress 1980a), and further in Lauraceae (e.g., Rohwer 1993) and Hernandiaceae (Kubitzki 1969; Endress and Lorence 2004). In Atherospermataceae and Calycanthaceae, inner staminodes persist during fruit development (Schodde 1969; Blake 1972).

Gynoecium

Carpels are free and have a superior ovary (except in *Gomortega* of Gomortegaceae and in *Tambourissa* of Monimiaceae, inferior and syncarpous; Endress 1980b; Kubitzki 1993). Carpel number ranges from 1 in Hernandiaceae (Kubitzki 1969) and Lauraceae (Rohwer 1993) up to 2000 in Monimiaceae (Lorence 1985)

In Calycanthaceae, there are two ovules per carpel with collateral placentation, positioned one on top of the other at anthesis (Blake 1972, Endress and Igersheim 1997); however, in core Laurales, there is only one, median, ovule per carpel (Endress and Igersheim 1997).

In Calycanthaceae, developmental studies on the gynoecium are scarce and have focused on *Calycanthus* (Erbar 1983; van Heel 1984). Nothing is known about gynoecium development of *Idiospermum*, despite its extremely large and unusual diaspore (naked embryos with 3-6 cotyledons; Blake 1972). In the pluricarpellate families of the core Laurales, studies of carpel development focused on one or only few species: one species of Monimiaceae (Sampson 1969a, Endress 1980a), one of Atherospermataceae (Sampson 1969b), and one of Siparunaceae (Endress 1972).

Aims of this thesis

The aim of **part 1** (Staedler et al. 2007) is to study the floral phyllotaxis and floral structure (androecium, inner tepals) of the Calycanthaceae. Of special interest are floral structural features associated with phyllotaxis (transition from vegetative to floral phyllotaxis, presence of organ series in spiral flowers). As there seems to be variation in the family, stamens are studied in the perspective of connective tip differentiation and anther dehiscence.

The aim of **part 2** (Staedler et al., in press) is to study gynoecium structure and development in Calycanthaceae, and to compare it with that of core Laurales. Two lines of enquiry are followed: a study of anthetic gynoecia in all genera, and a developmental study in a representative of both subfamilies of Calycanthaceae. Gynoecium morphology at anthesis and during development will be comparatively discussed in Calycanthaceae and in core Laurales.

The aim of **part 3** (Staedler and Endress, in press) is to study the diversity of floral phyllotaxis in the pluricarpellate families of the core Laurales, and to find connections between the different phyllotaxis patterns and other floral traits, such as flower size, shape, and organ number.

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FLORAL PHYLLOTAXIS AND FLORAL ARCHITECTURE IN CALYCANTHACEAE (LAURALES)

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Calycanthaceae are sister to the remainder of Laurales (magnoliid clade), an order seemingly showing high variability in floral phyllotaxis. Previous studies of floral phyllotaxis in this family focused on one species, *Calycanthus floridus*. Therefore, a comparative study of floral phyllotaxis, comprising species of all four genera of the family was undertaken. Floral phyllotaxis is spiral according to the Fibonacci pattern for all species studied. The more or less extensive transition zone from the vegetative decussate to the floral spiral phyllotaxis comprises three to nineteen organs. There is usually a gradual transition between floral organ types, especially between different functional parts of the perianth, and between stamens, staminodes and carpels. The transition between staminodes and carpels sometimes shows irregularities in organ sequence along the ontogenetic spiral. There is a tendency to form series of organs of the same kind in Fibonacci numbers. Thecae dehisce via laterally-hinged valves in *Sinocalycanthus*, but via simple longitudinal slits in all other genera. Food bodies are present on the stamens and inner tepals of *Calycanthus* and *Sinocalycanthus* but differ in extent. All previously described calycanthaceous fossil flowers (*Araripia*, *Virginianthus*, *Jerseyanthus*), appear to show spiral floral phyllotaxis. In the 3-dimensionally preserved *Virginianthus* and *Jerseyanthus*, arrangement of androecium organs in series of Fibonacci numbers appears to be present.

Keywords: Calycanthaceae, floral phyllotaxis, organ series, Fibonacci spiral, anthers, food body.

Introduction

Calycanthaceae, a small and distinctive family of basal angiosperms comprising four genera and ten species (Zhou et al. 2006) of temperate shrubs or tropical trees, have relatively large flowers (fig. 1), which are pollinated by beetles, thrips or flies (Grant 1950, Badrutt 1992, Vogel 1998, Worboys and Jackes 2005). The fossil record of reproductive structures of Calycanthaceae is relatively abundant (Mai 1987, Friis et al 1994, Herendeen et al. 1999, Mohr and Eklund 2003, Crepet et al. 2005) and goes back to the early Albian (Friis et al 1994). Some of these fossils are extremely well preserved (Crepet et al. 2005). Early studies recognized the affinity of Calycanthaceae to Monimiaceae s.l. and Lauraceae (Baillon 1868). This affinity was acknowledged in the major classification systems of the past 50 years: Cronquist (1957, 1981, 1988), Takhtajan (1959, 1987, 1997), Thorne (1974, 1992, 2000) and Dahlgren and Bremer (1985). Molecular phylogenetic analyses (Renner 1998, 1999, 2004, Qiu et al 1999, 2005, Soltis et al. 2000) settled the family as sister to the rest of Laurales. These analyses also divided the remaining Laurales into two clades of three families each: the Siparunaceae-Atherospermataceae-Gomortegaceae clade (85 species, Renner 2004) and the Monimiaceae-Hernandiaceae-Lauraceae clade (2750-3250 species, Renner 2004). Within Calycanthaceae, *Idiospermum* is sister to the rest of the family, and *Chimonanthus* is sister to the *Calycanthus*-*Sinocalycanthus* clade (Li et al. 2004, Zhou et al. 2006)).

From accounts on various groups of Laurales, it appears that their floral phyllotaxis is diverse. Floral phyllotaxis is, however, well documented only for some Hernandiaceae, Lauraceae, *Hortonia* of Monimiaceae and *Calycanthus floridus* of Calycanthaceae. Taxa studied in Hernandiaceae (Shutts 1959, Kubitzki 1969, Endress and Lorence 2004) and Lauraceae (Singh & Singh 1985, Endress 1987, Hyland 1989) show whorled phyllotaxis (exceptions with irregular phyllotaxis in few Lauraceae, Endress 1990). *Hortonia* (Monimiaceae) (Endress 1980b), *Calycanthus floridus* (Calycanthaceae) (Unger 1852, Baillon 1868, Eichler 1878, Prantl 1889, Erbar & Leins 1983) and *Chimonanthus praecox* (Calycanthaceae, only perianth studied, Nelson 1954) show spiral phyllotaxis. Information about floral phyllotaxis of the other families of the order is scanty and sometimes conflicting.

Floral phyllotaxis has been mapped on cladograms of basal angiosperms, either for the perianth (Zanis et al. 2003), or for the whole flower (Doyle and Endress 2000, Ronse De Craene et al. 2003, Endress and Doyle, 2007). These analyses show several transitions from spiral to whorled floral phyllotaxis and vice versa: in the branch leading to Nymphaeales, at the base of eudicots, at the base of the magnoliid clade, within Magnoliales and within Laurales. Calycanthaceae, at the base of Laurales are thus in a position close to such a transition. But, as former studies of Calycanthaceae were restricted to a single species, *Calycanthus floridus* (see above), and as basal angiosperms often show variability of floral phyllotaxis at various taxonomic levels (see Endress 1987, Doust 2001), a study on all genera of Calycanthaceae is needed.

Floral phyllotaxis often differs from vegetative phyllotaxis in a plant. This change, usually discrete in flowers with few organs, may be more gradual in flowers

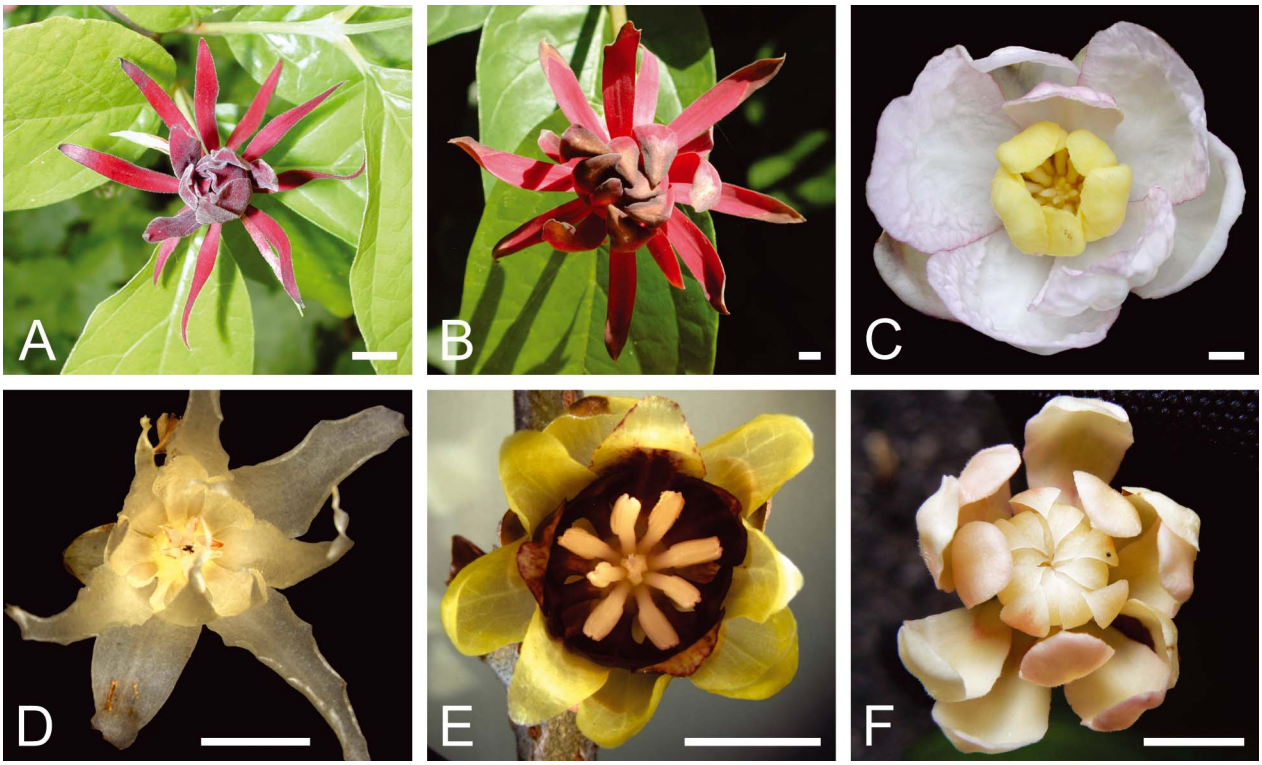


Fig. 1 Calycanthaceae flowers at anthesis. *Calycanthus floridus* (end of female phase). B, *Calycanthus occidentalis* (end of female phase). C, *Sinocalycanthus chinensis* (full female phase). D, *Chimonanthus nitens* (end of female phase-beginning of male phase). E, *Chimonanthus praecox* (full female phase). F, *Idiospermum australiense* (full female phase). Bar = 5mm.

with numerous organs. The notion of floral merism has usually been applied for whorled flowers. However, in spiral flowers, floral organs also tend to occur in preferred numbers and tend to appear in "series". A series is a set of organs of the same kind, relatively regularly surrounding the floral center. A series of a spiral flower corresponds to some extent to a whorl of a whorled flower, but appears less regular because the neighboring organs are not equidistant (in contrast to a whorl). Organs of an organ series appear in a number belonging to the mathematical series used to define the type of spiral phyllotaxis. In flowers showing Fibonacci spiral phyllotaxis, these numbers belong to the Fibonacci mathematical series (1, 2, 3, 5, 8, 13, 21…), such as described from some basalmost angiosperms (Endress 2001). In previous literature, the term "Kreis" (with quotes, Hirmer 1931) or the expression "Fibonacci cycles" (Nelson 1954) were used for series as we consider them. We prefer the term "series" because Kreis or cycle are sometimes also used for a whorled organization. The term cycle implies either a whorl or one full turn on the ontogenetic spiral. However the series represents more than one turn (approximately $1\frac{1}{2}$ turns for 5 organs, approximately $2\frac{1}{2}$ for 8 organs, etc.).

The average angle between two consecutively initiated organs of a series (α, the divergence angle) in a spiral system is linked to the mathematical series used to describe the system by the following relation: $\alpha = \lim_{n \to \infty} 360 ° \frac{U_n}{U_{n+1}}$ (with U_n a member of the mathematical series). For Fibonacci spiral phyllotaxis, the average divergence angle, also called the golden angle, is 137.50…°.

Calycanthaceae flowers have a floral cup, with different organs inserted at different sites on the cup. The perianth is inserted on the outer surface of the cup, up to its rim. Stamens are usually inserted on the rim, staminodes on the inside of the cup, and carpels (topographically) below the staminodes and at the bottom of the cup. This organization is present in all described species (Baillon 1868, Diels 1912, Rauh & Reznik 1951, Nicely 1965, Cheng and Chang 1963, Blake 1972, Dengler 1972, Wilson 1976). Other floral parameters vary substantially in the family in response to pollination ecology: from quite large beetle-pollinated trap flowers, to fly-pollinated, somewhat more open flowers (Delpino 1870, Grant 1950, Vogel 1998).

In this study six species from all four genera of Calycanthaceae were studied and compared in their floral architecture, floral phyllotaxis (including vegetative to floral phyllotaxis transition), and occurrence of organ series: two species each of *Calycanthus* and *Chimonanthus*, and the sole species of *Sinocalycanthus* and *Idiospermum*. We also focus on perianth and androecium structure, whereas gynoecium structure will be treated in a further study. Systematic aspects within the family and morphological interpretation of fossil calycanthaceous flowers based on the results on extant flowers are

discussed. Figure 1 introduces to the floral diversity of the family, Figures 2-8 relate to the single species, and Figures 9-14 provide comparisons throughout the family.

Material and Methods

The following collections were used for this study (S = Yannick M Städler; BGZ = cultivated in the Botanic Garden of the University of Zurich; organ number = collection used for calculation of average floral organ numbers).

Calycanthus floridus L. (one individual, BGZ): S004-71, S004-80, and S005-47 (organ number), S004-34 (fig. 2; fig. 8E), S004-4 (fig. 10A, 10D, 10G), S004-62 (fig. 13B, 13G, 13L), S004-80 (fig. 14E-H), S004-125, S004-150 (immature fruits), S005-94 (mature fruits with cup partially severed), S005-112 (intact mature fruit).

Calycanthus occidentalis Hooker & Arnott (one individual, BGZ): S004-111, S004-147, and 005-79 (organ number), S004-67 (fig. 3, fig. 8F), S005-48, S005-33 and S005-33 (fig. 10B, 10E, 10H), S004-157, S004-189 (immature fruits), S005-108 (mature fruit).

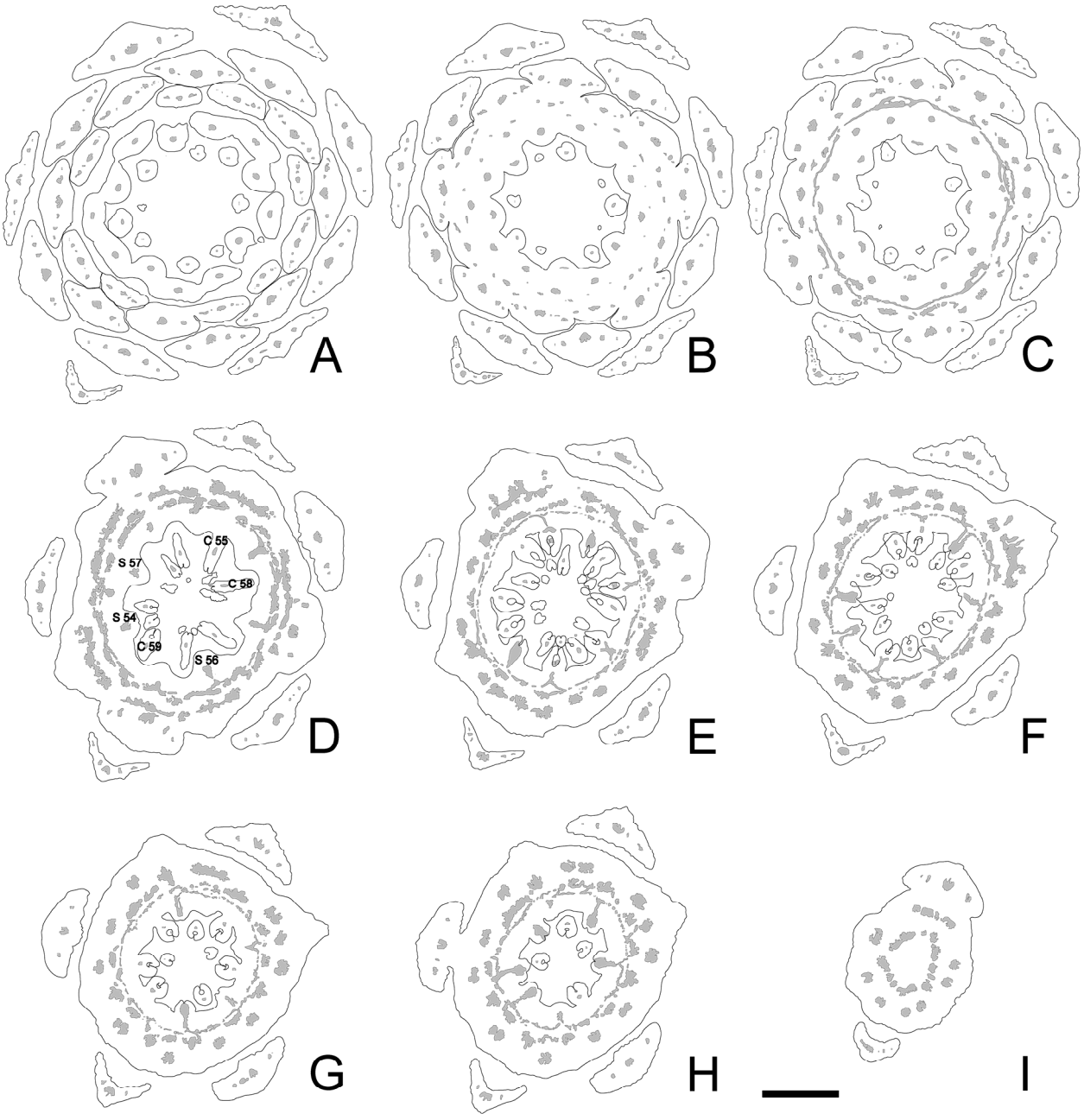


Fig. 2 *Calycanthus floridus*, transverse section series of late floral bud. Vasculature in grey. A, level of rim of floral cup. B and C, level of staminode-bearing part of floral cup. D-H, level of gynoecium. I, pedicel. S = staminode, C = carpel, number = floral organ number on the ontogenetic spiral. Bar = 1mm.

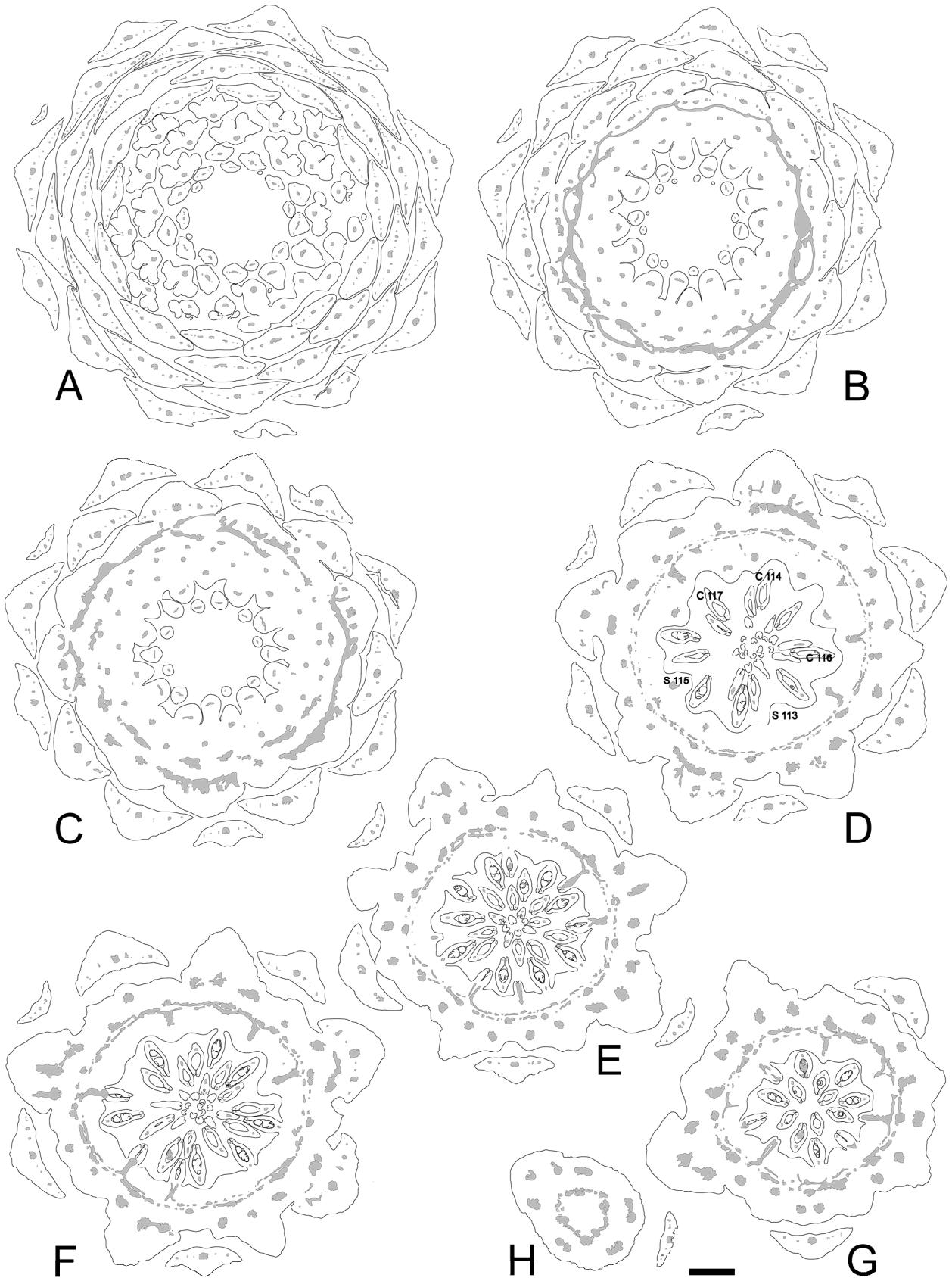


Fig. 3 *Calycanthus occidentalis*, transverse section series of late floral bud. Vasculature in grey. A, level of rim of floral cup. B and C, level of staminode-bearing part of floral cup. D-G, level of gynoecium. H, pedicel. S = staminode, C = carpel, number = floral organ number on the ontogenetic spiral. Bar = 1mm.

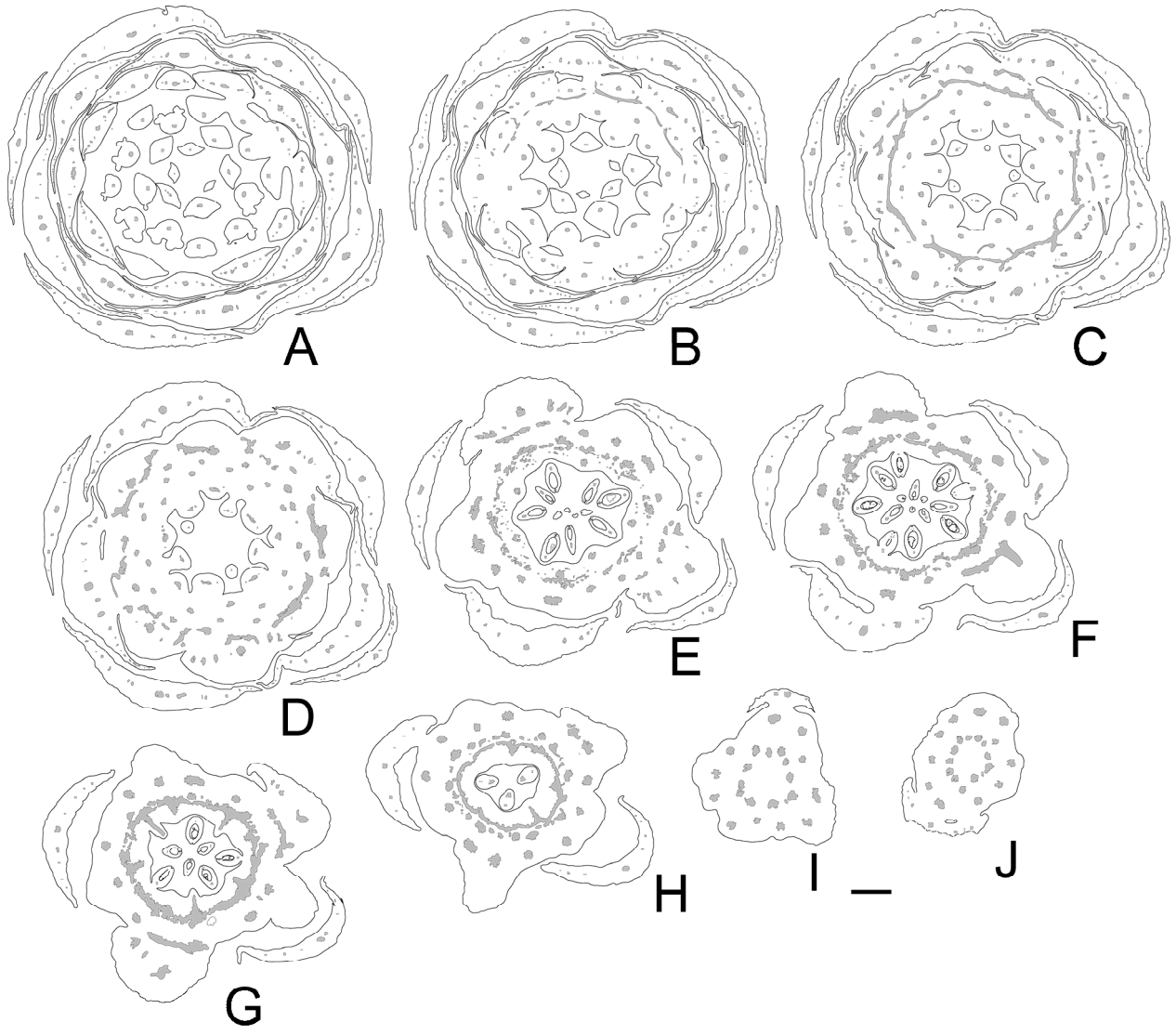


Fig. 4 *Sinocalycanthus chinensis*, transverse section series of late floral bud. Vasculature in grey. A, level of rim of floral cup. B-D, level of staminode-bearing part of floral cup. E-H, level of gynoecium. I and J, pedicel. Bar = 1mm.

Chimonanthus nitens Oliver (two individuals n°1&2, BGZ): JB Bachelier 004-136, 004-134, 004-198 (individual 1, fig. 11A, fig. 11D, fig. 11G); PK Endress 03-111 (individual 2, fig. 5; fig. 8A, 8A'); S004-231 (individual 1, organ number), S004-232 (individual 2, organ number).

Chimonanthus praecox (L.) Link (one individual, BGZ): PK Endress 04-3 (fig. 13C, 13H, 13M; organ number), PK Endress 03-112 (fig. 6; fig. 8B); S004-97, S004-131, and S004-163 (fig. 11B, 11E, 11H), S005-81 (immature fruits), S005-96, S006-7 (mature fruits).

Idiospermum australiense (Diels) S. T. Blake: BPM Hyland 2569 (Noah Creek, Northern Queensland, Australia; fig. 7; fig. 8C; fig. 15A-C); PH Weston NSW 607200, 004-10, 004-77, 004-79, 004-245, 005-84, 005-88 and 005-89 (Royal Botanic Gardens, Sydney; organ number), 004-8, 004-11 and 005-84 (Royal Botanic Gardens, Sydney; fig. 11C, 11F, 11I), 004-238 (fig. 13D, 13I, 13N); David H. Lorence 9471 NTBG 840223 (National Tropical Botanical Garden Kauai, Hawaii, USA: immature fruits).

Sinocalycanthus chinensis (W.C. Cheng & S. Y. Chang) W. C. Cheng & S. Y. Chang (three individuals: n°1-3, BGZ): S004-112 (individual 1, organ number), S004-92 (individual 2, organ number), S004-104 (individual 3, organ number), S004-56 (Individual 1, fig. 4; fig. 8D), S004-121 (fig. 9A, 9B; fig. 14A-D), S005-20 (individual 1, fig. 10C, 10F, 10I), S005-90 (individual 1, immature fruits), S005-97 (individual 1, mature fruits).

Plant material was fixed and stored in 70% ethanol. Serial microtome sections were made after embedding in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate) (Igersheim and Cichocki 1996). The sections were stained with toluidine blue and ruthenium red. For scanning electron microscopy (SEM) studies, specimens were critical-point-dried, sputter-coated with gold and studied at 20 kV with a Hitachi S-4000 scanning electron microscope.

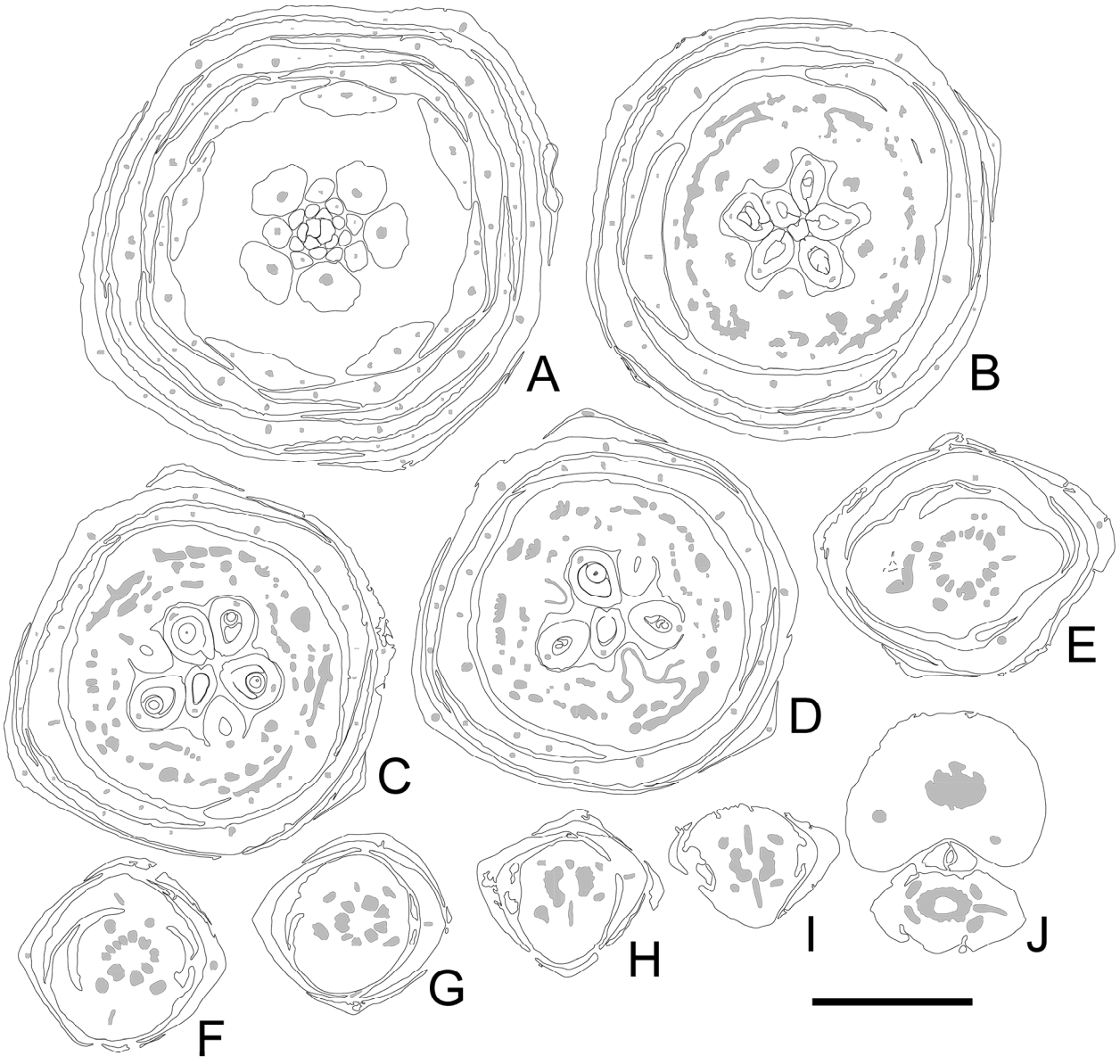


Fig. 5 *Chimonanthus nitens*, transverse section series of late floral bud. Vasculature in grey. A, level of rim of floral cup. B, level of base of staminodes. B-D, level of gynoecium. E-J, pedicel. Bar = 1mm.

For the study of phyllotaxis, the center of a flower needs to be determined. We did this in two ways. (1) If a transverse section comprises many densely packed organs, which is the case in the region of the rim of the floral cup of most species, the center of the flower is estimated to be between the three last initiated organs. (2) If a transverse section has relatively few, loosely packed organs, which is the case lower down in the floral cup, straight lines are drawn that more or less divide the floral cup in two halves, and the center of the floral cup is estimated from the intersections of these lines. In both cases, the relative position of organs is assessed using the center of the median vascular bundle of each organ in a transverse section close to, or just below, the base of the organ. These points of reference are then used to measure the angles between subsequent organs.

Divergence angles of the innermost organs conspicuously vary because of stochastic variation in the flower shape in its center, and measurement errors in determination of the flower center. We use an artificial boundary between phyllotaxis types based on statistical considerations. Systems are considered to show a decussate phyllotaxis when the divergence angles alternate from 90° to 180° ± 10°. Organs are considered to show Fibonacci spiral phyllotaxis if the average divergence angle equals the golden angle ± 1°, and if at least one of two consecutive angles falls within the interval of average divergence angle ± standard deviation. We will refer to organs belonging to the zone between the decussate phyllotaxis zone and the Fibonacci spiral phyllotaxis zone, as organs of the phyllotaxis transition zone.

The transition between leaves and bracts is gradual, we thus treated as bracts all the modified leaves in the vicinity

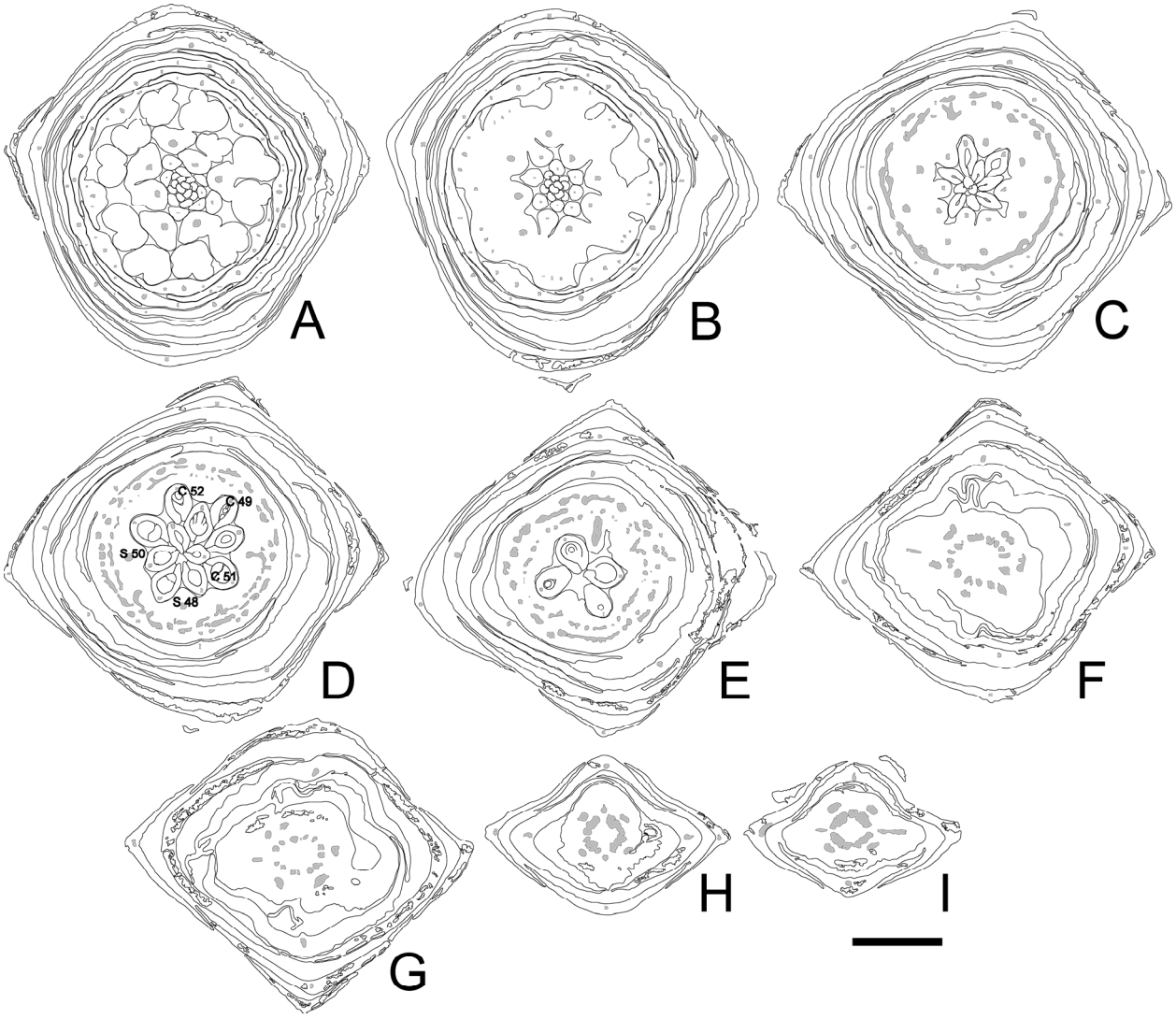


Fig. 6 *Chimonanthus praecox*, transverse section series of late floral bud. Vasculature in grey. A, level of rim of floral cup. B, level of staminode-bearing part of floral cup. C, level of base of innermost staminodes. C-E, level of gynoecium. F-I, pedicel. S = staminode, C = carpel, number = floral organ number on the ontogenetic spiral. Bar = 1mm.

of floral organs. The transition between bracts and tepals is gradual, with no precise delimitation. Endress (1980b, c) proposed (for spiral flowers of *Austrobaileya* and *Hortonia*) four criteria to - arbitrarily - set such a delimitation: "[…] (1) beginning of short internodes, (2) change of phyllotaxis from decussate to spiral, (3) beginning of an increase in size of the phyllomes, (4) beginning of branched vasculature in the phyllomes." (Endress 1980c). We have used phyllotaxis change to delimit bracts and tepals. The organs of the phyllotaxis transition zone have a protective function often until late in floral bud development and are often partially colored (white, yellow or red). They mostly play a role of "sepals" (in all genera except in *Calycanthus*) and occasionally a role of "petals" (in *Calycanthus floridus*), and they have thus been treated as tepals. We did not use the other criteria proposed by Endress (1980b,c) because they could not be applied to the family as a whole.

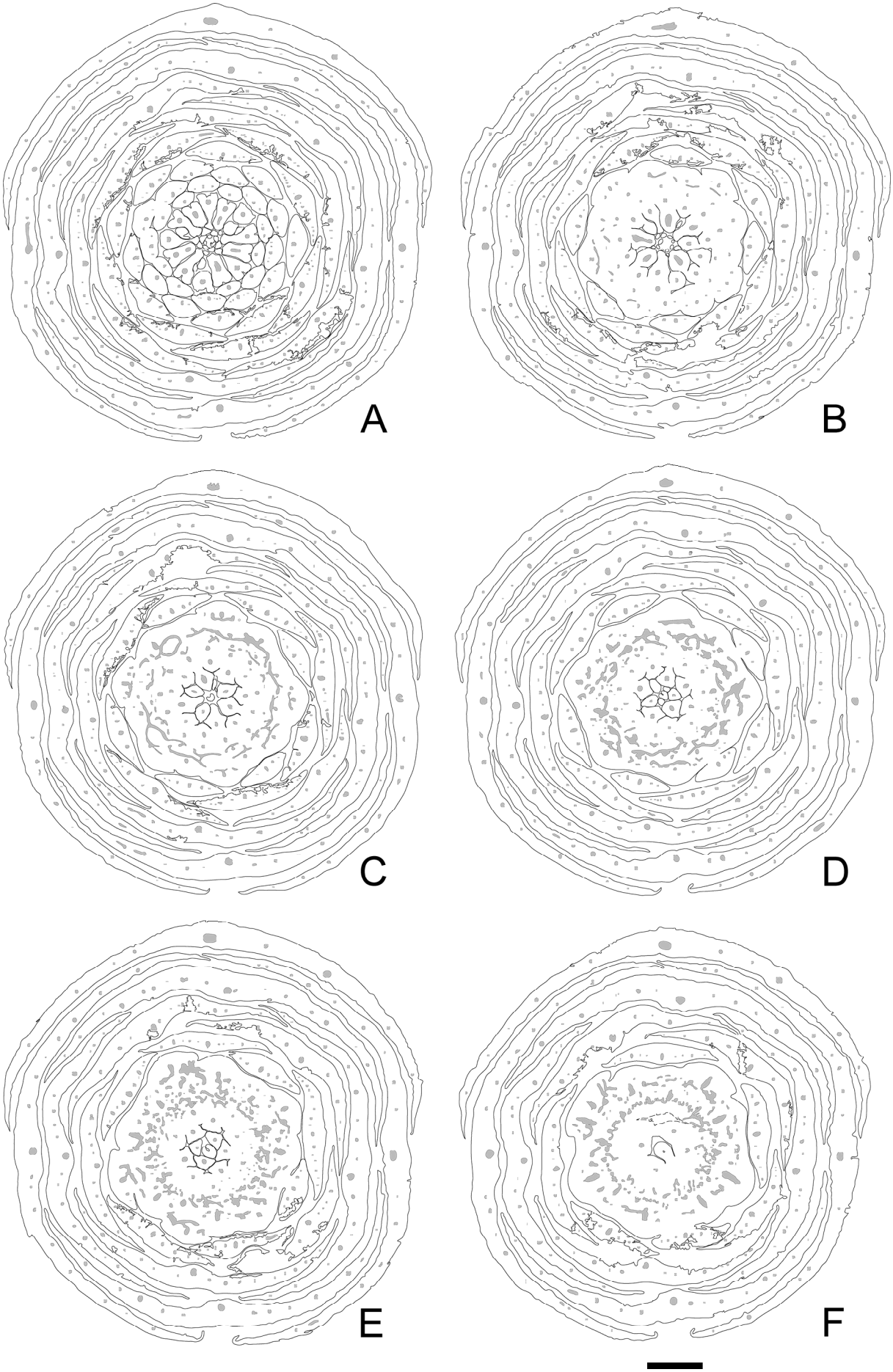
Floral organ numbers were counted for ten flowers per species and means, modes (printed in bold when present) and standard deviations calculated. Divergence angles were measured for a late floral bud of all studied species, and the mean angle and its standard error were calculated for each species. Divergence angles were cursorily examined in additional flowers of each species.

Results

Calycanthus floridus

Flowers are solitary in the axil of a leaf of the previous year and are preceded by a pair (or two pairs) of foliage leaves. Just before anthesis, stamens, staminodes and carpels are hidden by the tepals, and tepal tips are appressed to each other. The flowers are then ovate in LS and stigmas appear receptive. Tepals are dark reddish-brown. Progressive flower opening during anthesis (fig. 1A) is concomitant with style wilting and anther dehiscence.

In the sectioned floral bud studied for phyllotaxis (S004-43, fig. 2), the floral organs show Fibonacci spiral phyllotaxis, with an average divergence angle = 137.44° (±


A
B
C
D
E
F

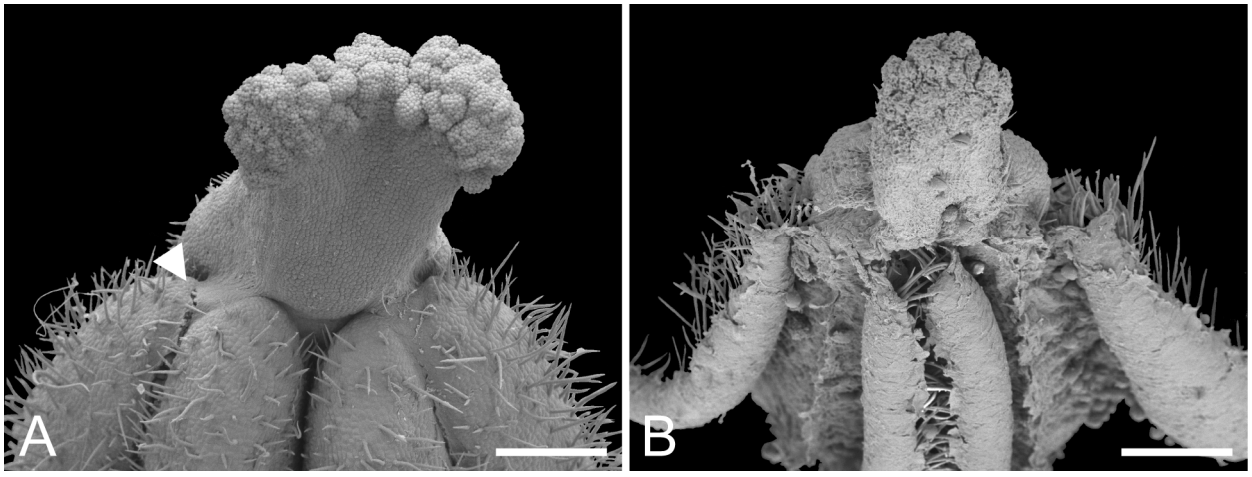


Fig. 8 *Sinocalycanthus chinensis*, laterally-hinged valves of stamens. A, late female phase of flowering, closed anther showing stomium following pollen sac outline bifurcating at the end of the pollen sac (white arrow). B, full male phase of flowering, open anther showing opened laterally hinged valves. Bar = 300µm.

5.51°) for the 80 innermost organs (all organs except decussate bracts and transition organs). Divergence angles between the innermost perianth organs show values all close to the golden angle (fig 12). Divergence angles between the remaining organs are also close to the golden angle (fig. 12). Two almost opposite organs are inserted on the pedicel of the floral bud (fig. 2I) (these organs alternate with the preceding pair of foliage leaves). The transition zone from decussate to spiral phyllotaxis comprises 3 organs (fig. 8E; fig. 10A, 10D). In later development, the ratio of floral organ to floral apex diameter decreases (fig. 10G). Unexpectedly, it was observed that along the ontogenetic spiral the first carpel is followed by the two last staminodes and only then by the remaining carpels (fig. 2D).

The ten studied flowering shoots (S004-71, S004-80, S005-47) comprise 2-4 (2.2 ± 0.6) leaves, two opposite-decussate bract-like organs (7 out of 10 shoots), (26-)**28**(-29) (27.7 ± 1) tepals, **13**(-16) (13.8 ± 1) stamens, (16-)**20**(-22) (19.2 ± 1.3) staminodes, and (25-)**34**(-35) (31.7 ± 3.6) carpels (the apparent modes of organ numbers are bolded; when no modes are apparent, all numbers given are in plain font). Nicely (1965) reported larger ranges of organ numbers: 15-30 tepals, 10-15(-20) stamens, 15-25 staminodes, 10-35 carpels (the numbers in Nicely (1965) for this and other species were reported as groups of five, which seems artificial). In the ten flowers here studied, tepals do not behave as expected from observation of the sections alone: at the end of the female phase of anthesis, a series of eight tepals (7.6 ± 1) are spreading, and later are reflexed, while the remainder at first stay upright and only later spread. The eight innermost tepals usually have an incurved apex. The arrangement of tepals in the sectioned floral bud (fig. 8E), and average tepal number of 28 in the ten buds studied, may indicate that the perianth is constituted of two 13-merous series (but see observation on anthetic flowers). Stamens usually form a 13-merous series, with often a less well-developed additional stamen behaving like a staminode (inflexed during the male phase of anthesis) (fig. 8E). Staminodes seem to form several 8-merous series at the rim of the cup (fig. 8E) and below (fig. 2B, 2C) (but see observations on fruits).

During fruit development (S004-125, S004-150), all staminodes enlarge, whereas all outer organs have abscised. The initially smaller innermost staminodes show the strongest growth in breadth and length and eventually becomeeven larger than the outer staminodes. Growth of the staminodes after anthesis results in the occlusion of the floral cup and complete inclusion of the carpels after wilting of the stigmas and styles. Staminodes form an approximately 21-merous series around the rim of the floral cup. In mature fruits (S005-94, S005-112), they become reflexed upon fruit desiccation, but this process does not open the floral cup enough to enable nutlet release. A mature fruit (S005-94) was found with the side of the floral cup mechanically severed, perhaps by a bird but apparently with no nutlets missing. Van der Pijl (1982) mentions dispersal of mature nutlets by squirrels.

Calycanthus occidentalis

Inflorescences are terminal with up to 15 flowers in a thyrsoid. After a variously long vegetative growth, the shoot apical meristem initiates a terminal flower preceded by a pair of at least partially reduced leaves, which may subtend two up to 7-flowered cymes. Up to four flowers in the inflorescence usually mature, the others usually abort. The flowers are similar in shape to those of *C. floridus* but larger and tepals are deep red (fig. 1B). Flowering proceeds like in *C. floridus*.

Fig. 7 *Idiospermum australiense*, transverse section series of late floral bud. Vasculature in grey. A, level of rim of floral cup. B, level of staminode-bearing part of floral cup. C-E, level of inner staminodes, and carpel. F, level of base of carpel. Bar = 1mm.

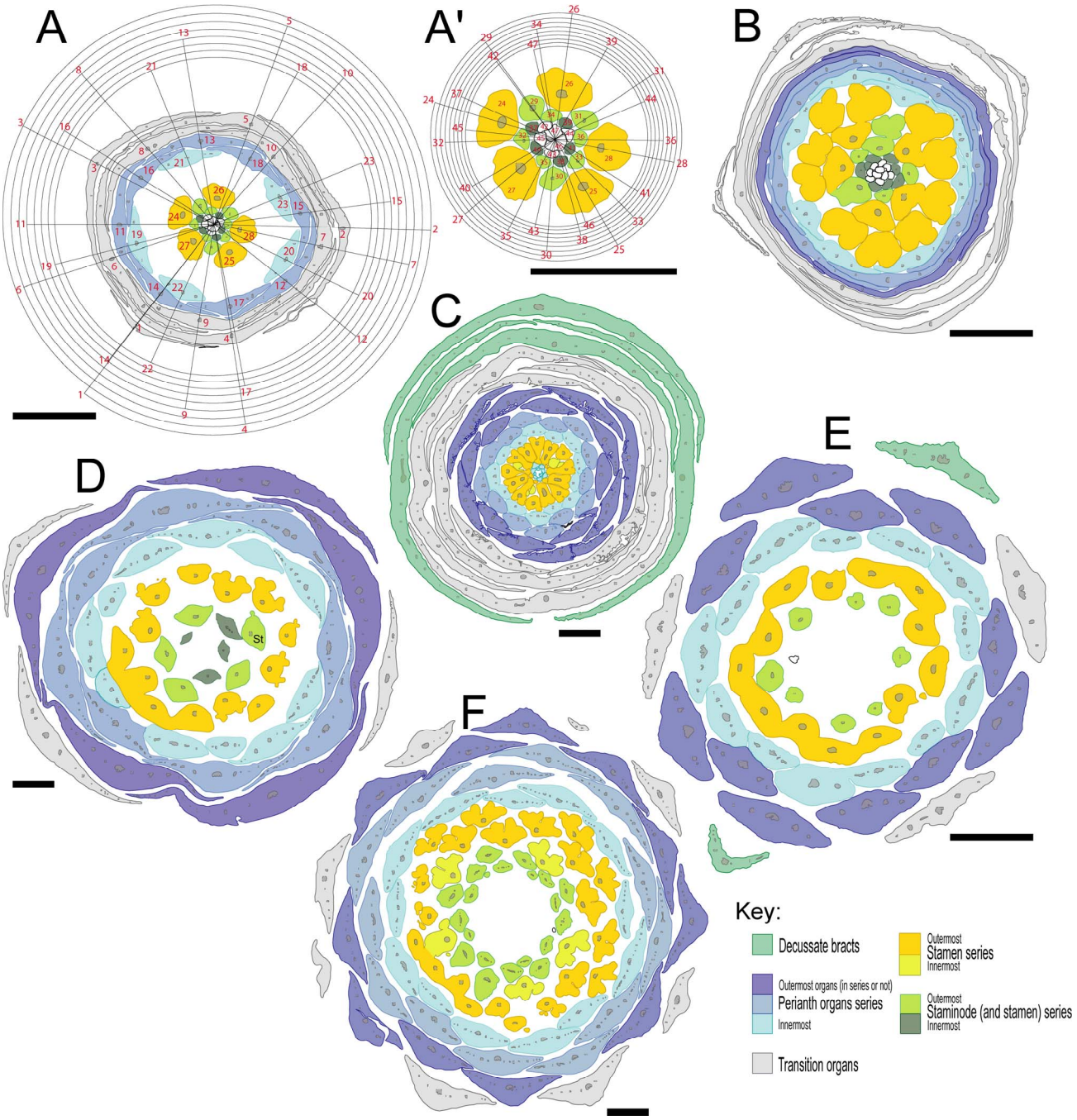


Fig. 9 Transverse sections at level of rim of floral cup, showing organ series. A, *Chimonanthus nitens*, with ontogenetic spiral and divergence angles shown for bracts and tepals. A', close-up of flower center, with ontogenetic spiral and divergence angles shown for stamens, staminodes and carpels B, *Chimonanthus praecox*. C, *Idiospermum australiense*. D, *Sinocalycanthus chinensis*. E, *Calycanthus floridus*. F, *Calycanthus occidentalis*. Bar = 1mm.

In the sectioned floral bud studied for phyllotaxis (S004-67, fig. 3), the floral organs show Fibonacci spiral phyllotaxis, with an average divergence angle = 137.48° (± 5.61°) for the 142 innermost organs (all organs except decussate bracts and transition organs). The divergence angles of the outermost floral organs and the innermost floral organs show the strongest deviation from the golden angle (fig. 12). The transition zone from decussate to spiral phyllotaxis comprises 9 organs (fig. 3F-H; fig. 8F; fig. 10B, 10E). In later development, the ratio of floral organ to floral apex diameter decreases (fig. 10H). Unexpectedly, along the ontogenetic spiral the first carpel is followed by the last staminode and only then by the remaining carpels (fig. 3D).

The ten flowers studied for organ numbers (S004-111, S004-147, and S005-79) were the terminal flowers of ten inflorescences. They comprise 0-2-4 (1.8 ± 0.9) opposite-decussate bract-like organs, (42-)**45-47**(-50)(46.1 ± 2.5) tepals, 22-27 (25.1 ± 1.6) stamens, 36-50 (41.6 ± 4.2) staminodes, and 35-43 (39.3 ± 3.7) carpels. Nicely (1965) reported much smaller organ numbers, but with larger ranges: 15-30 tepals, 10-15 stamens, 15-25 staminodes, 10-20 carpels. In the ten flowers here studied, no

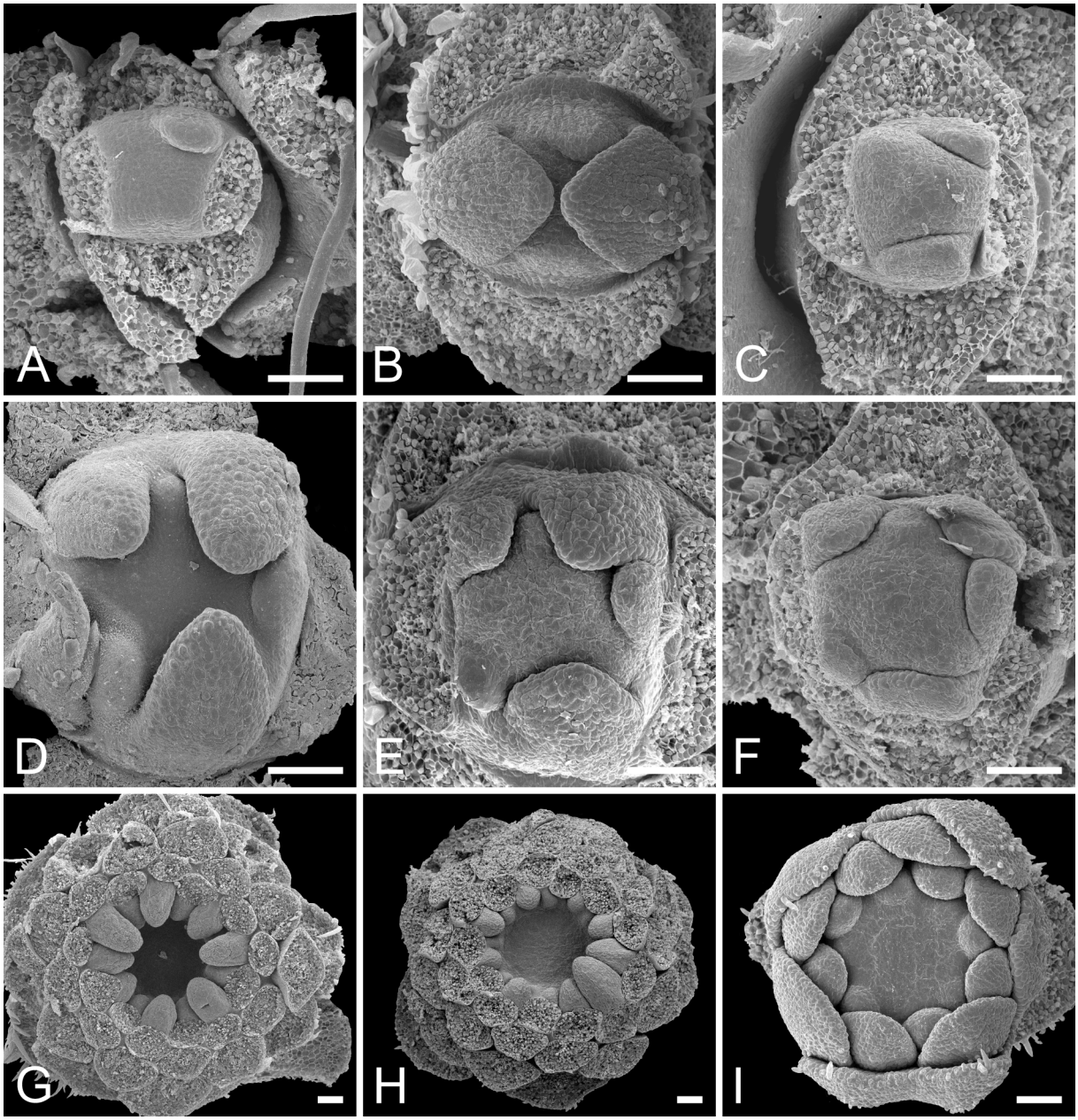


Fig. 10 Transition from decussate to spiral organ initiation: A, D, G, *Calycanthus floridus*. B, E, H, *Calycanthus occidentalis*. C, F, I, *Sinocalycanthus chinensis*. A-C, first organs of the transition zone. D-F, somewhat older: initiation of further organs of the transition zone. G-H, somewhat older, spiral initiation of organs. Bar = 100µm.

differentiation of the perianth into obvious series was observed during anthesis. In the sectioned floral bud, the perianth seems to be arranged in two or three 13-merous series (fig. 8F), but see observations on anthetic flowers. Stamens form two series in all flowers studied (also in the sectioned floral bud, fig. 8F). The two series show a different behavior during the male phase of flowering: the outer, 21-merous series reflexes during the male phase of anthesis, while the inner 3-5-merous series inflexes (like staminodes). In the ten flowers studied and in the sectioned floral bud, staminodes also appear to form two 21-merous series from their average number of 42 (Fig. 3B, 3C) (but see observations on fruits).

During fruit development, all staminodes enlarge whereas all outer organs have abscised. The initially smaller innermost staminodes show the strongest growth in breadth and length and become larger than the outer staminodes (S004-157 and S004-189). Growth of the staminodes after anthesis results in the occlusion of the floral cup and complete inclusion of the carpels after wilting of the stigmas and styles. In fruit, staminodes form two approximately 21-merous series on the rim of the floral cup. The staminodes desiccate during fruit maturation (observation on mature fruit S005-108); this process widely opens the cup, enabling nutlet release.

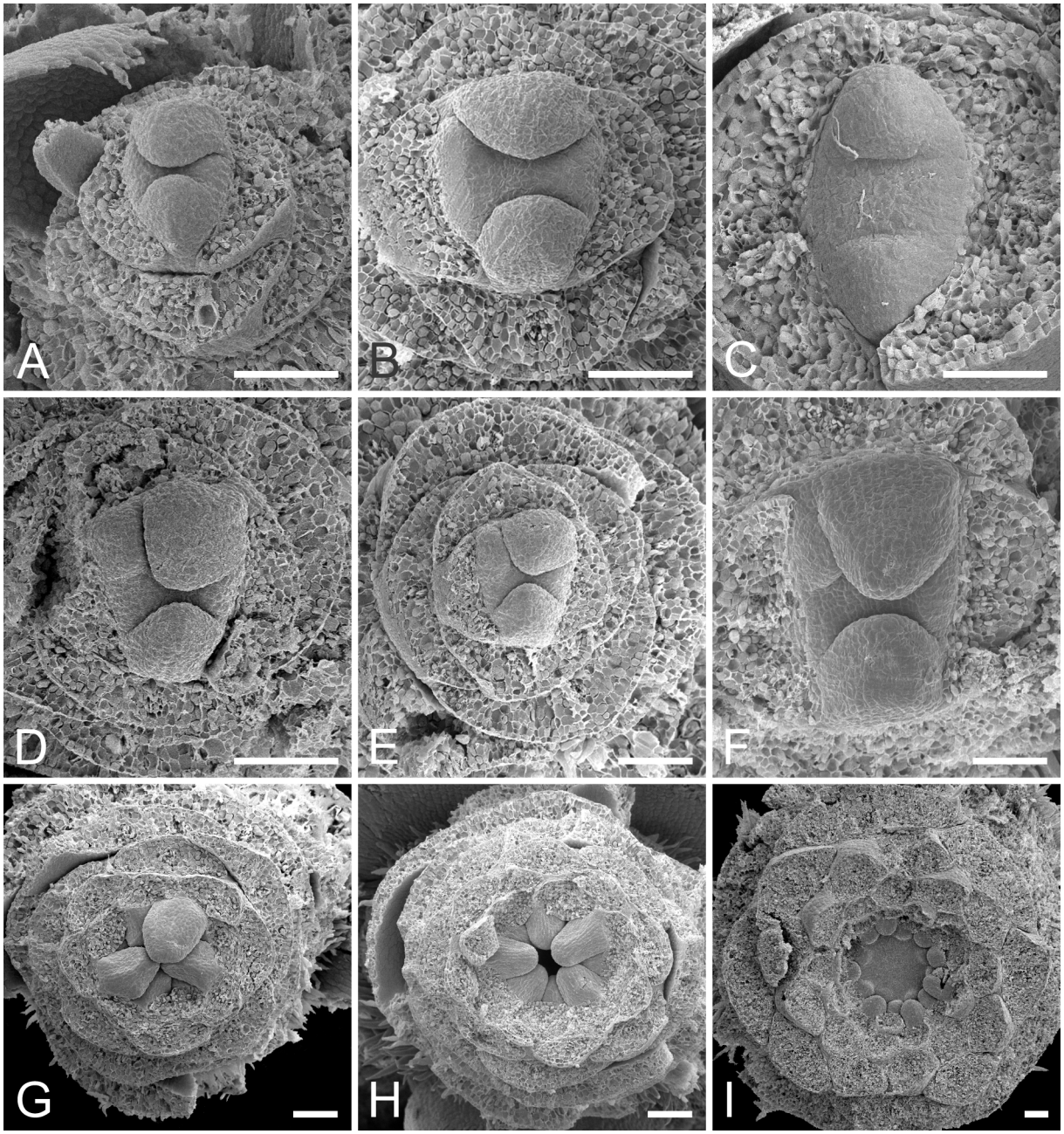


Fig. 11 Transition from decussate to spiral organ initiation: A, D, G, *Chimonanthus nitens*. B, E, H, *Chimonanthus praecox*. C, F, I, *Idiospermum australiense*. A-C, first organs of the transition zone, with scars of preceeding decussate organs visible. D-F, somewhat older: initiation of further organs of the transition zone. G-H, somewhat older, spiral initiation of organs. Bar = 100 μm.

Sinocalycanthus chinensis

Flowers are solitary and terminate long shoots. After vegetative growth, resulting in two to four leaf pairs, the shoot apex turns into the flower apex. At the beginning of anthesis, the white outer tepals are almost spreading and the yellow inner tepals form a rounded cup-like structure (fig. 1C). The reproductive organs are more or less exposed during anthesis.

In the sectioned floral bud studied for phyllotaxis (S004-56, fig. 4), the floral organs show Fibonacci spiral phyllotaxis, with an average divergence angle = 137.40° (± 6.06°) for the 68 innermost organs (all organs except decussate bracts and transition organs). Most divergence angles are close to the golden angle (fig. 12). The transition zone from decussate to spiral phyllotaxis comprises 5 organs (fig. 4I, 4J; fig. 8D; fig. 10C, 10F). In later development, the ratio of floral organ to floral apex diameter decreases (fig. 10I).

The ten flowers studied for organ number (3-4 of each of the three individuals; S004-92, S004-104, and S004-112) are preceded by two bract-like organs (8 out of 10 flowers), or bract-like organs are lacking (2 flowers), and comprise (22-)**26**(-28) (25.5 ± 1.9) tepals, **15**(-19) (16.3 ± 1.6) stamens, (14-)**15**(-17) (15.4 ± 0.9) staminodes, and (12-)**15**(-16) (14.4 ± 1.5) carpels. Cheng and Chang (1964) reported different ranges of organ numbers: 26-33 tepals,

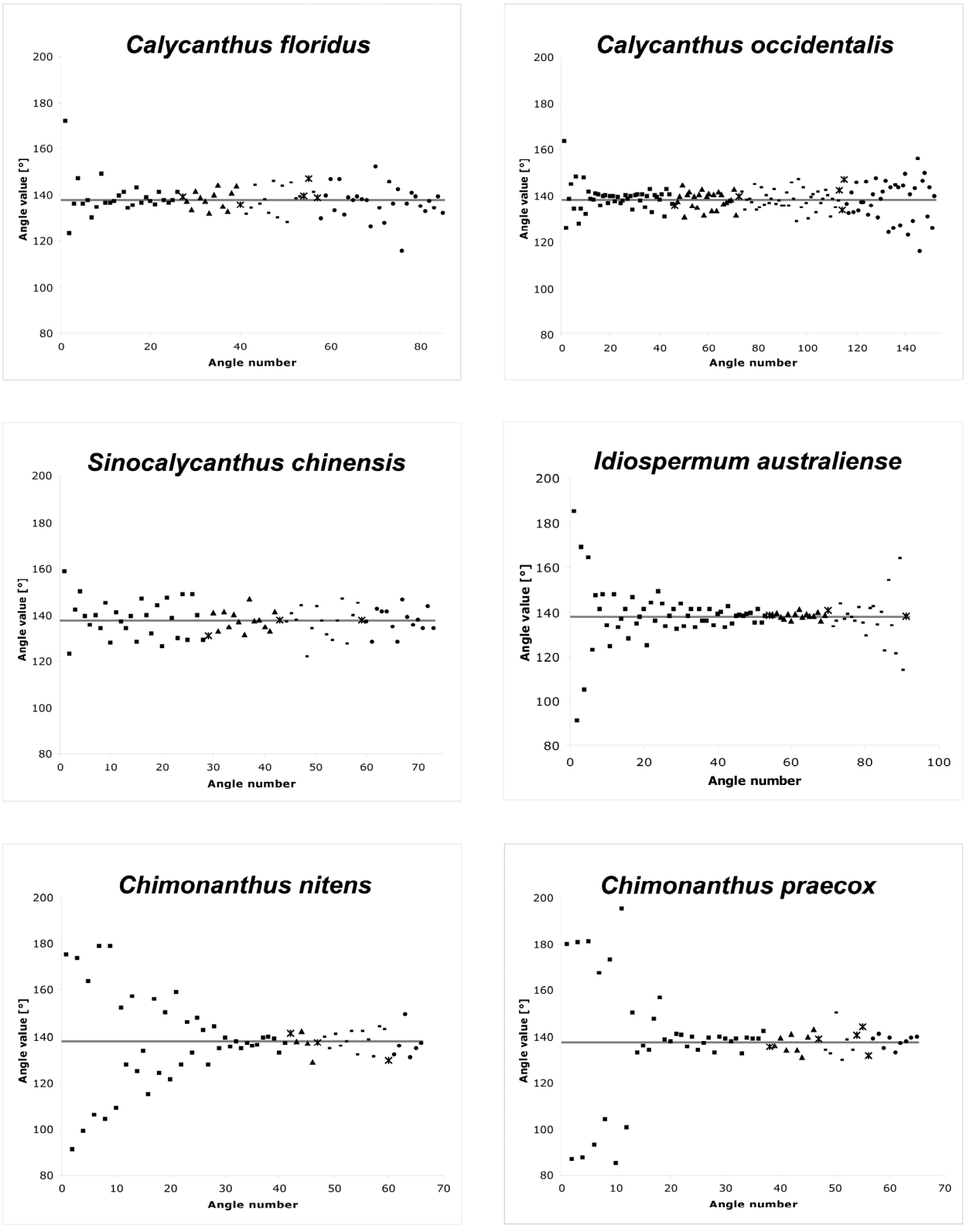


Fig. 12 Divergence angle value vs. angle number for all studied taxa. Squares: angles between tepals and/or bracts; triangles: angles between stamens; hyphens, angles between staminodes; circles: angles between carpels; asterisks: angles between different organ types. The horizontal line indicates the average divergence angle of the spirally arranged floral organs for each species.

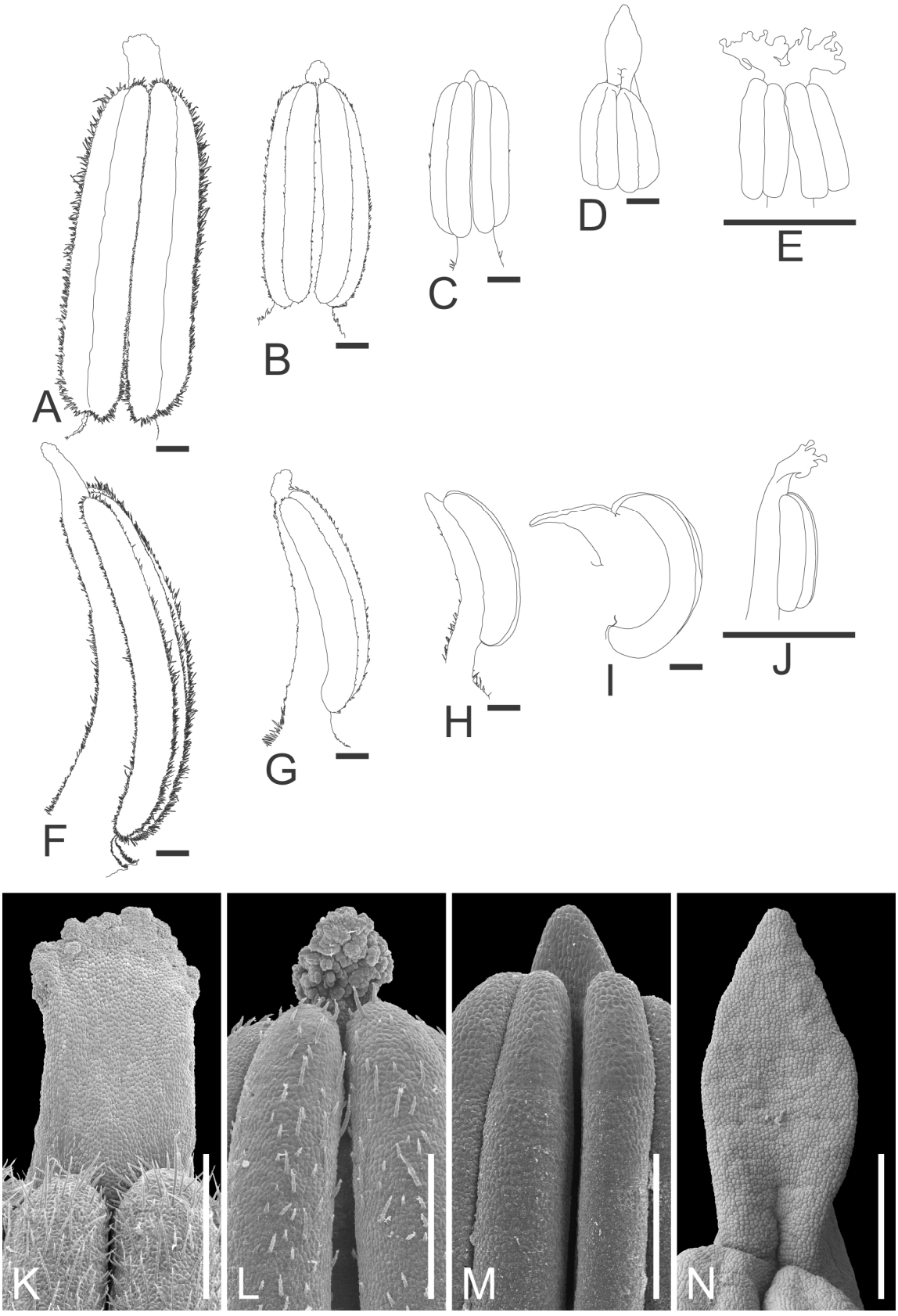


Fig. 13 Stamens and stamen tips of extant and extinct calycanthaceous genera: *Sinocalycanthus chinensis* (A, F, K), *Calycanthus floridus* (B, G, L), *Chimonanthus praecox* (C, H, M), *Idiospermum australiense* (D, I, N), and *Jerseyanthus calycanthoides* (E, J). A, D, G, J, M, dorsal view of stamens. B, E, H, K, N, lateral view of stamens. K-N, SEM micrographs of stamen tips, dorsal view. Bar = 500 µm.

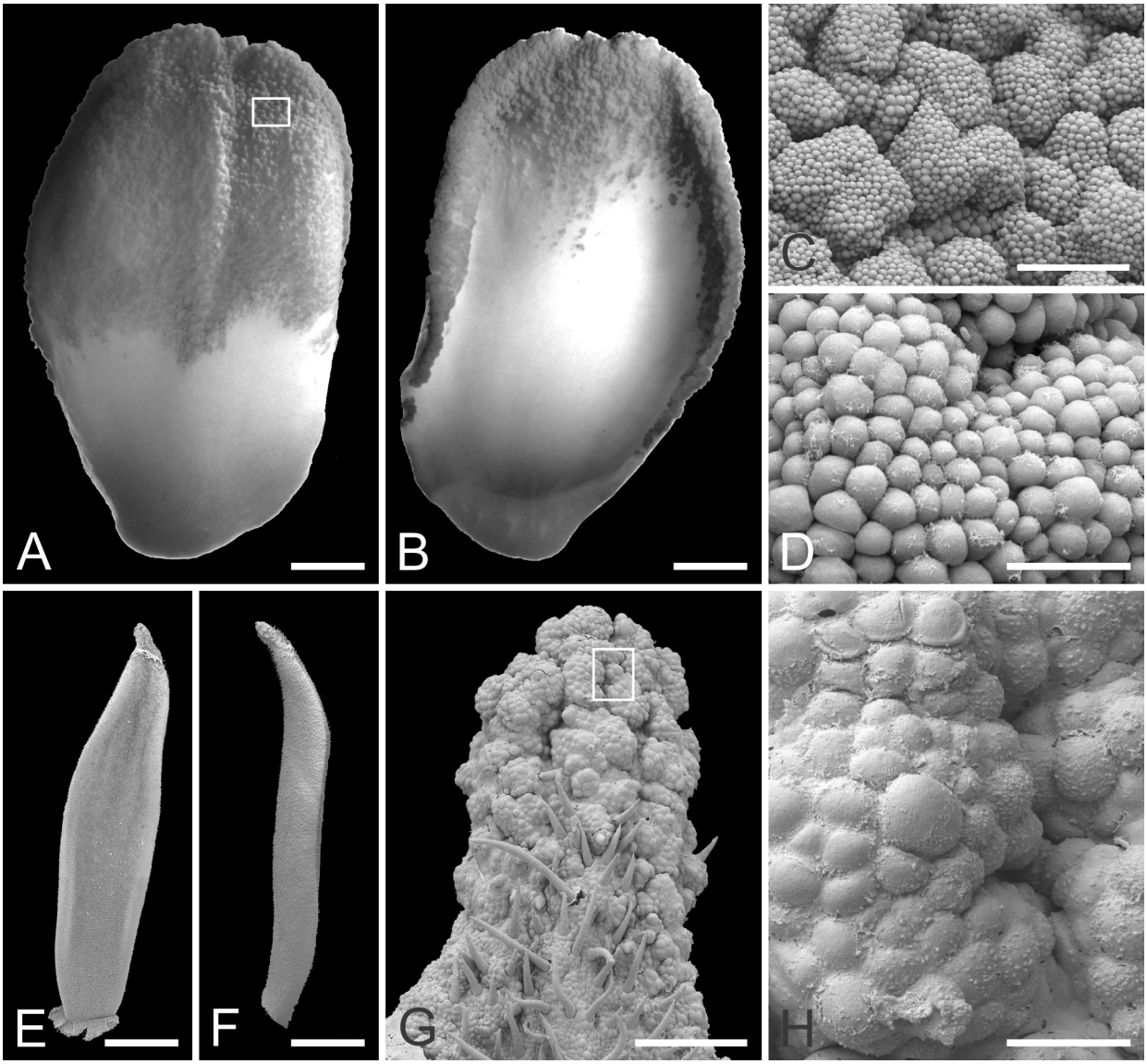


Fig. 14 Comparison of inner tepals in *Sinocalycanthus chinensis* (A-D) and *Calycanthus floridus* (E-H). A, B, photographs of the abaxial (A), and adaxial (B) side of an inner tepal of *S. chinensis*. C, D, SEM micrographs of the dorsal surface of an inner tepal (feeding tissue). E, F, SEM micrographs of the dorsal (E) and lateral (F) surface of an innermost tepal of *C. floridus*. G, H, detail of the tepal tip (feeding tissue). A, B, E, F, bar = 2mm. C, G, bar = 300µm. D, H, bar = 50 µm.

18-19 stamens, 11-12 staminodes, and 11-12 carpels. In the ten flowers here studied, the perianth is constituted of three approximately 8-merous series. The outermost series comprises mostly caducous sepaloid tepals (with one or two white petaloid members). The middle series is constituted of eight spreading, broad, thin and smooth, white tepals (fig. 1C). The inner series is constituted of eight upright, small, stout tepals (fig. 1C; fig. 14A, 14B), plus 1-2 smaller innermost tepals of similar shape. All these inner tepals are covered with a yellow papillate epidermis in their distal and lateral parts (fig. 14A-D), the remaining surface is smooth. The smooth part of the inner tepals is white except for two small red patches at their base. The inner eight tepals are coherent by secretion during the female phase of anthesis (fig. 1C). The extra one or two tepals could thus play a role in stiffening the inner tepal series by bridging neighboring tepals. During the male phase of anthesis, coherence of the inner tepals is lost as the tepals become slightly reflexed. In the sectioned floral bud, the perianth seems to form two approximately 8-merous series (fig. 8D) (but see observations on anthetic flowers). Stamens consistently form an outer series of 13 large, well-developed stamens, plus 2-3-4 smaller stamens that form a 5-merous series together with 3-2-1 staminodes (also in the sectioned floral bud, fig. 8D). The thecae do not open by single longitudinal slits but by valves, which originate by bifurcations of the dehiscence line at both of its ends (upper end shown in fig. 9A, 9B). In the sectioned floral bud, the staminodes not associated with stamens form an approximately 13-merous series (fig. 4C, 4D) (but see observations on fruits).

During fruit development, all staminodes enlarge whereas all outer organs have abscised (S005-90). The staminodes of the outer series do not usually show conspicuous growth, the staminodes of the inner series, on the contrary,

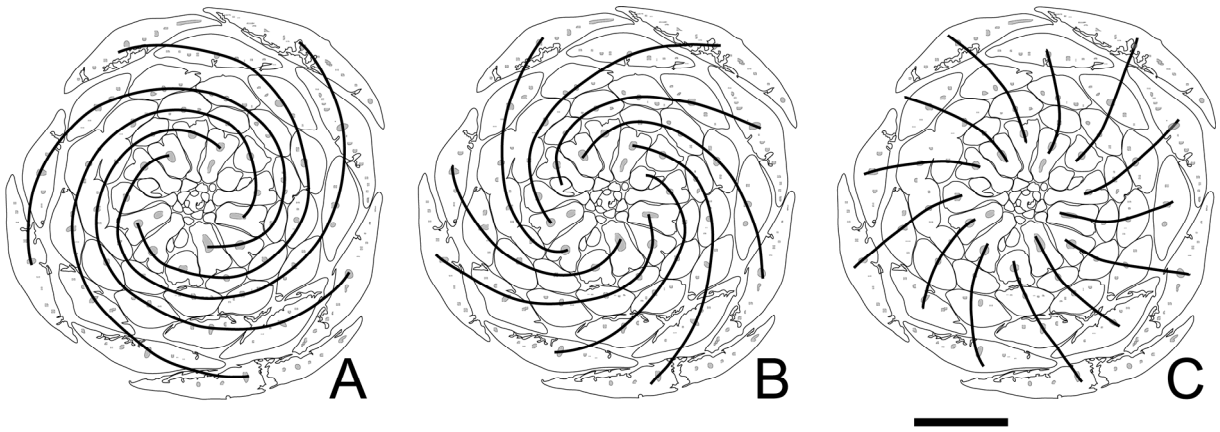


Fig. 15 *Idiospermum australiense*, transverse section of late floral bud, rim of the floral cup (from fig. 7A). Only the spirally arranged organs are shown, with different sets of parastichies. A, set of 5 parastichies. B, set of 8 parastichies. C, set of 13 parastichies. Bar = 1mm.

conspicuously enlarge, ultimately leading to the occlusion of the floral cup and complete inclusion of the carpels after wilting of the stigmas and styles. The enlarged staminodes become reflexed upon fruit desiccation (S005-97). This process is associated with a widening of the orifice of the cup, which enables nutlet release.

Chimonanthus nitens

Flowers are solitary in the axis of evergreen foliage leaves. The stamens and stigmas are exposed during anthesis. The flowers are narrowly funnel-shaped at early anthesis. The whitish petaloid tepals progressively spread to an almost horizontal position during anthesis (fig. 1D). Three outer tepals reflex during anthesis.

In the sectioned floral bud studied for phyllotaxis (Endress 03-111, fig. 5), the floral organs show Fibonacci spiral phyllotaxis, with an average divergence angle = 137,83° (± 4.38°) for the 37 innermost organs (all organs except decussate bracts and tepals of the transition zone). Divergence angles between the last floral organs initiated show the strongest deviation from the golden angle (fig. 12). The sectioned floral bud comprises ten decussate organs; the transition zone from decussate to spiral phyllotaxis comprises nineteen organs (fig. 5B-E; fig. 8A; fig. 11A, 11D). In later development, the ratio of floral organ to floral apex diameter does not conspicuously decrease (fig. 11G).

The ten flowers studied for organ number (five in each of the two specimens, S004-231 and S004-232) comprise 8-**10** (9.5±1.2) decussate bracts, **2**-**4**-5 (2.8±1.4) sepaloid tepals, 2-**3**-5 (3 ± 0.9) recurved petaloid tepals, 13-19 (15.9 ± 1.9) not recurved petaloid tepals, **5**-6 (5.2 ± 0.4) stamens, 10-**11**-**12** (11.3 ± 0.3) staminodes, and **7**-9 (7.6 ± 0.7) carpels. Nicely (1965) reported similar organ numbers but with larger ranges: 10-20 tepals, 5 stamens, 5-12 staminodes, 5-15 carpels. In the ten flowers here studied, the exposed part of bracts and sepaloid tepals is brownish and hard, these organs are most likely not involved in pollinator attraction. The petaloid tepals form several series with varying patterns. The outermost, recurved petaloid tepals usually form a 3-merous series. The middle petaloid tepals are the largest and the longest, they form either two 5-merous series or only one 8-merous series (as in the sectioned floral bud, fig. 8A). The innermost tepals are shorter, slightly clawed, they form a 5-merous series in all flowers studied (also in the sectioned floral bud, fig. 8A). The stamens form a 5-merous series in most flowers studied (also in the sectioned floral bud, fig. 8A), an additional, smaller stamen is however present in 3 of the 10 flowers studied. In the sectioned floral bud the staminodes seem to form an outer 8-merous and an inner 5-merous series (fig. 5B, fig. 8A').

The role of the staminodes in fruit construction, and fruitlet dispersal has not been studied, as fruiting material was not available.

Chimonanthus praecox

Flowers are solitary in the axil of fallen foliage leaves of the preceding season. The stamens and stigmas are exposed during anthesis. The flowers are broadly funnel-shaped at early anthesis. They comprise yellow and brownish-red petaloid tepals (fig. 1E), the yellow ones spread to a more or less horizontal position during anthesis.

In the sectioned floral bud studied for phyllotaxis (Endress 03-112, fig. 6), the floral organs show Fibonacci spiral phyllotaxis, with an average divergence angle = 137.78° (± 3.79°) for the 46 innermost organs (all organs except decussate bracts and transition organs). Most organs show divergence angles close to the golden angle (fig. 12). The sectioned floral bud comprises 6 decussate organs, the transition zone from decussate to spiral phyllotaxis comprises 13 organs (all tepals in fig. 6E, the 12 outer tepals in fig. 6D and fig. 6C, the 10 outer tepals in fig. 6B; the 9 outer tepals in fig. 8B; see also fig. 11B, 11E). In later development, the ratio of floral organ to floral apex diameter does not conspicuously decrease (fig. 11H). Unexpectedly, along the ontogenetic spiral the first carpel is followed by the last staminode and only then by the remaining carpels (fig. 6C).

The ten flowers studied for organ number (Endress 04-3) comprise 12-**14**-16 (14.4±1.3) decussate bracts, 5-**6**-7 (6.4±0.9) sepaloid tepals, 15-**16**-18 (16.1 ± 0.9) petaloid tepals, 6-**8** (7.3 ± 0.9) stamens, 8-12 (10.4 ± 1.4)

staminodes, and 8-**9**-**10** (9.3 ± 0.7) carpels. Nicely (1965) described similar organ numbers, but with larger ranges: 15-20 tepals, 5-10 stamens, 10-15 staminodes, 5-15 carpels. In the ten flowering shoots here studied, the 21 first organs (decussate bracts and phyllotaxis transition tepals) are short, broad-based organs with a tip that is hard and brown (the last organs before the petaloid tepals are yellow and petaloid at their base), these organs do not seem to be involved in pollinator attraction. The petaloid tepals of the ten studied flowers form on the average two 8-merous series (also present in the sectioned floral bud, fig. 8B). The first, outer series comprises all the elongate, yellow tepals. The second, inner series, comprises all the short, clawed, partially or entirely brownish-red tepals (see also Nelson 1954). The red-brownish tepals secrete nectar by small glands (nectarioles, Vogel 1998). The two innermost perianth series, together with the stamens represent the optical attractant (fig. 1E) and reward system of the flower. The stamens often form an 8-merous series (six of the ten flowers studied), or a series of 6 or 7 stamens and 2 or 1 staminode (in the sectioned floral bud, seven stamens are present, fig. 8B). The remaining staminodes approximately form an 8-merous series (also in the sectioned floral bud, fig. 8B; fig. 6C).

During fruit development (S005-81), all staminodes enlarge whereas all outer organs have abscised. Growth of the staminodes after anthesis results in the occlusion of the floral cup and complete inclusion of the carpels after wilting of the stigmas and styles. Staminodes show no movement during fruit desiccation. Fruitlets may be released through decay of the tissue of the staminodes (S005-96). Mature fruits were found with the cup mechanically severed (vertically slashed) and the nutlets missing (S006-7), probably taken by birds.

Idiospermum australiense

The flowers are terminal or axillary, solitary, or in botryoids of 3 to 11 flowers, or in thyrsoids (personal observation of Y.S. on herbarium and living material). At the beginning of anthesis, the anthers and stigma(s) are hidden (Worboys and Jackes 2005); the flowers are obovate in LS. During anthesis, the flowers progressively open. At the end of anthesis, most tepals are spreading or are recurved (fig. 1F). Tepals are creamy white at first and become progressively flushed with pink, then red and finally dull reddish purple.

In the sectioned floral bud studied for phyllotaxis (Hyland 2569, fig. 7), the floral organs show Fibonacci spiral phyllotaxis, with an average divergence angle = 137.67° (± 6.38°) for the 78 innermost organs (all organs except decussate bracts and transition organs). The last initiated organs show the largest deviation from the golden angle. Divergence angles close to the golden angle are observed for the innermost perianth series and for the stamen series (fig. 12). The sectioned floral bud comprises four decussate organs and nine organs in the transition zone from decussate to spiral phyllotaxis (fig. 8C; fig. 11C, 11F). In later development, the ratio of floral organ to floral apex diameter decreases (fig. 11I).

The ten studied flower buds (Weston NSW 607200, 004-10, 004-77, 004-79, 004-245, 005-84, 005-88 and 005-89) comprised **6**-**10**-12 (8.6 ± 2.3) bract-like organs, 32-**35**-**38**-48 (38.2 ± 4.4) tepals, **13**-14-15-**16** (14.2 ± 1.4) stamens, **13**-**16**-**18**-**21** (16.2 ± 3.1) staminodes, and 0-**1**-**2** (1.2 ± 0.8) carpels. Blake (1972) reported: 30-40 tepals, 13-15 stamens, 8-10 staminodes, 0-2 carpels. Worboys (2003) reported 32-48 tepals, 10-17 stamens, 8-23 staminodes and 1-5 carpels in newly found southern populations. Wilson (1976) reported: 48-50 tepals, 12-13 stamens, 8-10 staminodes, 0-2 carpels. In the ten late floral buds and flowers here studied, the caducous decussate bracts serve to protect the young floral bud. The following 20 tepals are either caducous bud protection organs, non-caducous spatulate, reflexed, optical and olfactory display organs (Worboys and Jackes 2005), or non-caducous intermediate organs between these two types. These tepals may be arranged in 3 series of 8 or 5 organs (fig. 8C). The innermost tepals form consistently two series of 13 tepals (also in the sectioned floral bud, fig. 8C). The outer series of 13 tepals comprises mostly spreading, large, spatulate, clawed, olfactory and optically attractive organs, and 2-3 smaller, thicker, acuminate tepals (fig. 1F). The innermost 13 tepals are vertical, short, stout, with parallel and straight margins, and an incurved broadly acuminate apex (fig. 1F). These tepals seem to be involved in the construction of the sheltered environment of the floral center characteristic for the observed beetle pollination (Worboys and Jackes 2005). A series of 13 stamens is almost always present on the rim of the cup (fig. 8C), and an additional series of 3 seemingly functional, smaller stamens sometimes inside the cup, topographically just below the first stamen series (also present in the sectioned floral bud, fig. 8C). The frequent staminode numbers (13, 16, 18, 21) may indicate one or two series (21 staminodes were found in the sectioned floral bud). Staminodes close the cup at the end of the female phase of anthesis (Worboys and Jackes 2005). This could play a role in protection against predation by the numerous larvae found in the flowers (Worboys and Jackes 2005). Staminodes persist until quite late in fruit development, as observed on immature fruits (Lorence 9471 NTBG 840223) (see also Endress 1983). But they play no role in diaspore release as only one fruitlet develops, and the entire fruit is the diaspore. Most flowers of the collection by PH Weston from a cultivated tree (Weston NSW 607200, 004-10, 004-77, 004-79, 004-245, 005-84, 005-88 and 005-89) comprise one carpel (5/12) or two carpels (5/12); few had no carpel (2/12). In the collection from a wild tree by BPM Hyland (Hyland 2569), flowers with two carpels were rare (less than 10% of the studied flowers), and around half of the flowers had only one carpel; the rest had no carpel. Because we favored large late buds, this could be a collecting artefact (if flowers with two carpels are indeed larger than flowers with only one or no carpel) or it might reflect the less competitive environment of the cultivated plant than the wild tree from which the specimens were collected.

Discussion

Floral Architecture

Flowers of Calycanthaceae are either open at anthesis (*Chimonanthus*, fig. 1D, 1E), or are closed during the female phase and later open during the male phase (*Calycanthus*, *Idiospermum*, fig. 1A, 1B, 1F), or contain a sheltered but not completely closed chamber that opens at the transition from female to male phase, as the tips of the tepals move apart from each other (*Sinocalycanthus*, fig. 1C). Flowers always have a floral cup, on the upper rim of which stamens are borne. Staminodes are always positioned at the entrance of the floral cup. The ovary is always hidden in the cup (fig. 2-7), with stigmas exposed during the female phase of anthesis (*Chimonanthus*, *Sinocalycanthus*), or hidden (*Calycanthus*, *Idiospermum*). The presence of a floral cup is also pronounced in other Laurales (Endress 1990a, Endress and Igersheim 1997).

An outstanding feature found in this study is that the thecae in *Sinocalycanthus* open via laterally-hinged valves, and not simple longitudinal slits as in the other Calycanthaceae studied (fig. 9A, 9B). *Sinocalycanthus* flowers have the largest stamens of studied Calycanthaceae (fig. 13A-J), with an especially large connective, a feature found to be correlated with valvate dehiscence (Hufford and Endress 1989). This is of special interest because this opening mode is present in a number of Magnoliales (Endress and Hufford 1989), but occurs rarely in Laurales (Endress and Hufford 1989). As it is also common in fossil Cretaceous stamens (Friis et al. 1991) and present in the Cretaceous genus *Jerseyanthus* (fig. 13E, 13J) (see below) our new results may give additional weight to an interpretation of such anthers as plesiomorphic in Laurales.

Floral Phyllotaxis and Transition between Floral Organs

All Calycanthaceae flowers here studied show spiral phyllotaxis according to the Fibonacci pattern. Optimization studies (Doyle and Endress 2000, Zanis et al. 2003, Ronse de Craene et al. 2003, Endress and Doyle, 2007) indicate that the ancestral character state may be whorled for the perianth in the magnoliid clade (a clade comprising two subclades of two orders each: the Laurales-Magnoliales subclade and the Piperales-Canellales subclade, Qiu et al. 1999, 2000, Zanis et al. 2002). Both spiral and whorled floral phyllotaxis are also present in the Magnoliales as well as in more basal angiosperms (Doyle and Endress 2000, Endress and Igersheim 2000, Endress 2001). This suggests two main alternative hypotheses: (1) the ancestral floral phyllotaxis in magnoliids is whorled, and a transition to spiral phyllotaxis has occurred early in the evolution of Laurales, probably at least at the early-middle Albian (to which *Virginianthus calycanthoides* belongs, the earliest known fossil with Calycanthaceae-like flowers and probably with spiral phyllotaxis, Friis et al. 1994). Whorled floral phyllotaxis in Laurales is known since the early Cenomanian from the Lauraceae-like flowers of *Mauldinia* (Drinnan et al. 1990). (2) The ancestral floral phyllotaxis in magnoliids is spiral, and whorled floral phyllotaxis among magnoliids evolved independently several times. To test these hypotheses more rigorously, future studies of floral phyllotaxis in other families of Laurales and other magnoliids are needed.

The transition zone from vegetative to floral phyllotaxis extends over 11-19 organs in *Chimonanthus*, 9 organs in *Idiospermum* and *Calycanthus occidentalis*, and 3-5 organs in *Calycanthus floridus* and *Sinocalycanthus* (fig. 12). Flowers of *Chimonanthus* need 5-7 months from initiation to anthesis, and the floral apex in the early spiral phase is about 100-150μm in diameter (fig. 11D, 11E). In contrast, flowers of *Calycanthus* and *Sinocalycanthus* need 3-4 months from initiation to anthesis, and the floral apex in the early spiral phase is about 200-300μm in diameter (fig. 10D-F). Thus, transitions with many organs appear to be correlated with relatively small and slow growing floral apices, whereas transitions with only few organs appear to be correlated with relatively large and fast growing floral apices. A large organ primordium size relative to the floral apex may have an inhibitory role in the transition process by allowing less placement freedom for the new primordium. The growth rate of the floral apex seems to play a crucial role in phyllotaxis transition.

The transition from one organ type to the nextone is unidirectional in flowers of Calycanthaceae. However in the transition from staminodes to carpels, irregularities in organ identity sequence were found in three taxa (*Calycanthus floridus*, *C. occidentalis*, and *Chimonanthus praecox*). The first carpel preceded the last staminode or the two last staminodes on the ontogenetic spiral (fig. 2D; fig. 3D; fig. 6C). Despite the irregularities in sequence of organ identity, the positions of the organs are very close to ideal Fibonacci positions. During the initiation of the last staminodes, and the first carpels, the now concave floral apex has reached its maximal size, which could explain the observed irregularities. Apparently, under such extreme conditions organ identity depends rather on the local, sectorial neighborhood than on the position on the ontogenetic spiral, if subsequent organs are small and not contiguous. Shorter plastochrons than in the perianth could contribute to emphasize such a phenomenon. Such extreme cases with minute size of the organ primordia and large size of the floral or shoot apex would favor a view as proposed by Plantefol (1949) who focused on parastichies rather than the ontogenetic spiral as determinants for organ initiation. Similar irregularities in sequence were also found and discussed in heads of Asteraceae, here with regard to bracts, ray flowers, and disk flowers (Hirmer 1931, Bachmann 1983, Battjes and Bachmann 1996, Battjes and Prusinkiewicz 1998). As these systems are entire inflorescences, they are larger than single flowers and therefore easier accessible for experimental studies.

The easy switch from staminodes to carpels and vice versa may suggest that staminodes of Calycanthaceae are in their identity closer to carpels than to stamens, thus strengthening the view of Hiepko (1965) who based his hypothesis that the staminodes of Calycanthaceae should rather be interpreted as carpellodes on observations he made on young stages: the distinct transition between stamens and staminodes, but the impossibility of distinguishing between staminodes and carpels. However, the presence of organs with only one, very reduced pollen

sac, especially in taxa with numerous stamens (*Calycanthus*, *Sinocalycanthus* and *Idiospermum*), similar behavior of fertile stamens and staminodes during anthesis, do not support a carpel identity, at least of the outermost staminodes. It seems reasonable to suggest that the staminodes of Calycanthaceae have a distinct morphology, and that they may be intermediate organs between stamens and carpels (as a side effect of spiral organization) that have acquired a new function in the closure of the floral cup. Gene expression studies would be needed to resolve the identity of these organs decisively.

Organ Series

The perianth organs of Calycanthaceae, although they are always arranged following a continuous spiral, show differentiation into functional categories (bud protection vs. attraction, reward or construction of a sheltered environment for pollinators). The differentiation of the perianth almost always includes the presence of intermediate organs, in accordance with the fading borders model of floral developmental genetics (Buzgo et al. 2004, 2005). Organs can nevertheless be grouped into subcategories. The organ number of a subcategory is often a Fibonacci number (see Nelson 1954, for the perianth of *Chimonanthus praecox*). The innermost perianth organs seem to always be involved in pollinator attraction, sometimes including reward (*Ch. praecox*, probably also *Sinocalycanthus*, see Vogel 1998, for both taxa), and sometimes in the construction of a shelter for pollinators. The latter is the case in the beetle flowers of *Calycanthus* (Grant 1950, Nicely 1965, Badrutt 1992), and *Idiospermum* (Worboys and Jackes 2005), and could also be the case in *Sinocalycanthus* (personal observation of small Coleoptera and Heteroptera between the reflexed outer stamens and the inner tepals in female phase flowers at night).

Stamens, more often than other organs, appear in series: series of 5 or 8 in *Chimonanthus*, series of 13 in *Calycanthus floridus*, *Sinocalycanthus*, and *Idiospermum*, and series of 21 in *Calycanthus occidentalis* (fig. 8A-F). Few additional, often reduced inner stamens are present in *Calycanthus*, *Sinocalycanthus*, and *Idiospermum*. They form a series with staminodes (fig. 8D). The regularity of stamen number is probably due to the developmental constraints of their position on the rim of the floral cup. The outer and the inner stamen series sometimes do not behave similarly during anthesis, the inner series tends to behave like staminodes: in *Calycanthus*, they inflex at the end of anthesis, thus contributing to floral cup closure (whilst the outer stamens reflex).

Staminodes often appear in series of a higher Fibonacci number than stamens (usually 13 or 21): this is probably due to their late initiation, when the floral apex is at maximal size, and their relatively narrow shape. The staminodes always play a role in the closure of the floral cup during fruit development and often during anthesis (Worboys and Jackes 2005, this study). At fruit maturity, they reopen the cup and allow nutlet release in at least two taxa (*Calycanthus occidentalis* and *Sinocalycanthus*), and may play this role also in *C. floridus*. Staminode decay may also play a role in nutlet release in *Chimonanthus praecox*. In *Idiospermum*, the staminodes and even the stamens seem to persist until late fruit maturation. At maturity, the staminodes disintegrate together with the floral cup.

Floral Structure and Intrafamilial Relationship

Two recent phylogenetic studies of Calycanthaceae, using nrITS (Li et al. 2004), and combining ITS, *trn*L-F and *trn*C-D (Zhou et al. 2006), have confirmed affinity of most of the genera of the Calycanthaceae (Cheng and Chang 1963, 1964, Blake 1972): *Sinocalycanthus* sister to or nested in *Calycanthus*, *Chimonanthus* sister to *Calycanthus* plus *Sinocalycanthus*, and *Idiospermum* sister to the remainder of the family. Segregation of *Calycanthus chinensis* into a separate genus, *Sinocalycanthus*, (Cheng et Chang 1964), was based on differences in the perianth (breadth, color, and surface differentiation of tepals, see above, fig. 1A-C), and lack of smell of the flowers (although this does not correspond to our observations). Other differences between *Sinocalycanthus* and *Calycanthus* include: valvate dehiscence of the anthers of *Sinocalycanthus* (this study) vs. dehiscence by slits in *Calycanthus* (Endress and Hufford 1989) and all other extant Calycanthaceae (this study), postgenital coherence of inner tepal series. Instead of discrete conical food bodies (fig. 14E-H), "feeding tissue" (papillate, cytoplasm-rich tissue similar to that of the food bodies on inner tepal and stamen tips in *Calycanthus*) is present on the yellow inner tepal periphery and partially on stamen and staminode tips (Vogel 1998, this study: fig. 14A-D). All of these characters can be interpreted as autapomorphies of *Sinocalycanthus* but none of them can be interpreted unequivocally as autapomorphies of *Calycanthus*.

In contrast, successful hybridization between *S. chinensis* and *C. floridus* (Lasseigne et al. 2001) suggests a placement of *Sinocalycanthus* in *Calycanthus*. The feeding tissue of *Sinocalycanthus* (tip of the inner tepals, stamens and staminodes, fig. 13K; fig. 14A-D) is present on the same organs at the same place as the food bodies of *Calycanthus* (fig. 13L; fig. 14E-H), and they seem to differ only in size, and maybe in amount of secretion produced (much more abundant in *Calycanthus* fig. 14D, 14H). Feeding tissue is not present on the petal and anther tips in *Chimonanthus* and *Idiospermum* (fig. 13M, 13N). The postgenital coherence of the inner tepals during the female phase of anthesis (present only in *Sinocalycanthus*) could be correlated with production of secretion by the "feeding tissue" during the female phase, and its cessation during the male phase (concomitantly with continuous opening of the flower). *Calycanthus* flowers smell of fermented fruits and are pollinated by small Coleoptera (Grant 1950, Badrutt 1992). Although Cheng and Chang (1964) described the flower of *Sinocalycanthus* as scentless, we detected a faint smell of overripe pears that appeared to be stronger at night. At night, flower visitors were observed in a cultivated plant, among which were a few small, yet undetermined Coleoptera. These observations are consistent with the putative generalized cantharophily of these flowers, predicted by Vogel (1998) and thus for a close functional similarity of the flowers of *Calycanthus* and *Sinocalycanthus*. Another functional similarity is the wide

fruit opening in C. *occidentalis* and *Sinocalycanthus chinensis* at maturity. These structural/functional similarities support the close relationship of *Sinocalycanthus* and *Calycanthus* found in molecular studies.

Interpretation of Fossil Calycanthaceous Flowers

The new results on floral structure in Calycanthaceae can be used to improve the interpretation of the floral structure of fossil calycanthaceous flowers.

Araripia florifera is based on an impression fossil of a flowering twig with 6(-7) flowers (2 probably mature and 4-5 in earlier stages of development) of the early Cretaceous (Aptian or possibly Albian) of the Crato Formation, Brazil (Mohr and Eklund 2003). The largest flower or flower bud is about 10 mm long and 6 mm broad, it comprises at least 11-13 helically arranged strap-like tepals with appressed tips, the tepals are inserted on a floral cup comprising at least six to seven globular structures. These flowers or floral buds are reminiscent of early female phase *Calycanthus floridus* flowers. A side view of a flower of *C. floridus* (in early female phase or just before anthesis) displays a similar number of tepals to those seen in the fossil. The tepals of the fossil seem spirally arranged, but the mode of preservation prevents any detailed observations.

Virginianthus calycanthoides is based on a single well-preserved charcoalified flower of the early Cretaceous (early-middle Albian) of Virginia, USA (Friis et al. 1994). The flower is about 2.8 mm long and 2.2 mm broad, phyllotaxis is probably spiral, but preservation does not allow identification of series, except for staminodes (an 8-merous series), and perhaps for the perianth that comprises at least 12 tepals in two series (perhaps a 5-merous and an 8-merous series), the exact number of stamens is not known (30-40), the anthers are extremely extrorse and dehisce via laterally-hinged valves.

Jerseyanthus calycanthoides is based on extremely well preserved charcoalified clearly calycanthaceous fossil flowers from the late Cretaceous (Turonian) of New Jersey, USA (Crepet et al. 2005). The flowers are 1.3-2.8 mm long and 1.5-3 mm broad. The perianth parts are numerous and appear spirally arranged, although no full set of parastichies could be drawn from the illustrations. The androecium was described as comprising a whorl of 12 "staminode-stamen pairs" with each "staminode" abaxial to and overarching a latrorse to extrorse stamen (Crepet et al. 2005). However, 13 stamens could be present in CPC 1487 (Figs. 1-3 in Crepet et al. 2005). In extant Calycanthaceae, no trace of whorled arrangement was found in any part of the flowers, but series of 13 stamens were consistently found in *Calycanthus floridus*, *Sinocalycanthus*, and *Idiospermum*. In *Idiospermum*, the rim of the floral cup is crowded with organs (tepals and stamens); successive sets of parastichies rapidly increase in steepness (fig. 10A-C); as the organs are dorsiventrally flattened, the parastichies of the set of 13 look almost like orthostichies (fig. 15C). Thus each outer stamen is almost - but not exactly - on the same radius as one of the innermost tepals (the theoretical angle between a tepal and its nearest stamen is 12.4°). If the stamens and "outer staminodes" of *Jerseyanthus* were spirally arranged, the "outer staminodes" and the stamens would not be perfectly aligned, which indeed appears to be the case (fig. 11 and 13 in Crepet et al. 2005). In conclusion, *Jerseyanthus* flowers are most likely spiral, because of the following reasons: (1) absence of any whorled phyllotaxis in the studied extant members of the family, (2) the common occurrence of series of 13 stamens in extant Calycanthaceae, (3) presence in *Jerseyanthus* of a set of 13 steep parastichies almost (but not completely) like orthostichies as in extant Calycanthaceae (especially *Idiospermum*, fig. 15C). The perianth of Calycanthaceae often shows conspicuous differentiations between its outer and inner organs (*Idiospermum*, *Chimonanthus*, and *Sinocalycanthus*). The inner tepals of *Sinocalycanthus* are short and have a papillate epidermis on most of their surface(fig. 14A, 14B). What has been interpreted as "outer staminodes" in *Jerseyanthus* also shows these features. Given their morphological similarity to similarly placed organs of flowers of the extant Calycanthaceae, we suggest that the "outer staminodes" of *Jerseyanthus* should rather be considered as tepals. The two thecae of the anther of *Jerseyanthus* open via laterally-hinged valves ("staminal dehiscence 'valvate' (dehiscence slit I-shaped…",Crepet et al. 2005) and have a modern counterpart in *Sinocalycanthus*, as found in this study, whereas the thecae of the anthers in all other extant Calycanthaceae appear to open with single longitudinal slits. An additional unusual feature of the anthers in *Jerseyanthus* is a ramified connective appendage, which may represent food bodies (fig. 13E, 13J) (Crepet et al. 2005). All extant Calycanthaceae have connective appendages, but they are not ramified, only in *Sinocalycanthus* there may be incipient ramification (fig. 13A-D, 13F-I, 13K-N).

Detrusandra mystagoga is based on charcoalified flowers of the late Cretaceous (Turonian) of New Jersey (Crepet and Nixon 1998), with additional flowers found in central Georgia from the Santonian (Herendeen et al. 1999). The flowers are 1.0-2.5 mm long and 1.1-3.2 mm broad. Despite superficial resemblance to Calycanthaceae, the fossil was placed by a cladistic analysis close to Eupomatiaceae (Crepet and Nixon 1998). Character states consistent with exclusion from Calycanthaceae are the following: scalariform perforation plates of the vessel elements, laminar introrse stamens, absence of staminodes, bilobed, sessile stigmas and at least five ovules per carpels (Crepet and Nixon 1998). Character states of *Detrusandra mystagoga* that are inconsistent with membership of the crown group of Eupomatiaceae are: presence of a perianth, well developed floral cup that totally encloses the carpels, and completely apocarpous carpels. Nevertheless, this fossil could still belong to the stem group of the Eupomatiaceae. Spiral floral phyllotaxis of *Detrusandra* does not help in the systematic placement, as it is also spiral in both Calycanthaceae and Eupomatiaceae (Endress 2003).

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COMPARATIVE GYNOECIUM STRUCTURE AND DEVELOPMENT IN CALYCANTHACEAE (LAURALES)

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Calycanthaceae, sister to all other Laurales, are the most distinct family of the order in their gynoecium structure (lateral placentation, presence of two ovules). Gynoecium structure was studied in a representative of each genus of Calycanthaceae, and gynoecium development in a representative of each of the two subfamilies (Calycanthoideae and Idiospermoideae). Newly found shared features are postgenital coherence between the free carpels (extragynoecial compitum), abortion of the upper of the two ovules, and lobation of the outer integument. Differences in reproductive structures between the two subfamilies are reviewed. Newly found differences include: carpel primordium shape, contribution of the outer integument to micropyle formation, epidermis differentiation of the rim of the integuments, and mode of formation of the compitum. Unexpectedly, at anthesis, ovary and ovules of *Idiospermum* are not larger than those of Calycanthoideae, despite the conspicuous difference in fruit. The identity of "staminodes" (sterile organs between stamens and carpels) is discussed. Sterile carpel-like structures (carpellodes) are documented in *Idiospermum*. The lateral ovule position in Calycanthaceae is correlated with a different development of carpel closure as compared to core Laurales, which exhibit median ovule position. Gynoecium morphology of fossil Calycanthaceae and its implications for gynoecium evolution in Calycanthaceae and Laurales are discussed.

Keywords: Calycanthaceae, Laurales, Idiospermum, gynoecium development, carpel development, compitum.

Introduction

Calycanthaceae are sister to the remainder of Laurales (core Laurales) (Renner 1999, 2004, Qiu et al. 2005) and comprise about seven species in four genera of temperate shrubs and tropical trees (Nicely 1965, Blake 1972, Cheng and Chang 1964, Li and Bartholomew 2007). Within Calycanthaceae, the deepest split is between the tropical monotypic tree *Idiospermum australiense* (Idiospermoideae), and the temperate shrubs of the rest of the family (Calycanthoideae) (Li et al. 2004, Zhou et al. 2006); the split between the two subfamilies has been estimated to be at least 70 Million years old (Zhou et al. 2006).

What makes Calycanthaceae unique in Laurales are features of the gynoecium: (1) ovule number and placentation differ from all other Laurales, and (2) the seeds in *Idiospermum* have the largest embryos known in angiosperms (Blake 1972, Endress 1983). The gynoecium of Calycanthaceae is apocarpous with 1-40 spirally arranged carpels (Nicely 1965, Blake 1972, Cheng and Chang 1964, Staedler et al. 2007). The carpels are borne on the bottom of an extensive floral cup (Baillon 1868, Cheng and Chang 1964, Blake 1972) (Fig. 1). In some flowers, a gynoecium is lacking altogether (Blake 1972, Staedler et al. 2007). The stigmas are secretory and vary in morphology between the two subfamilies (Endress and Igersheim 1997). An extragynoecial compitum was reported for some Calycanthaceae (Endress and Igersheim 1997). The carpels are largely plicate but possess a short ascidiate base (Schaeppi 1953, Leinfeller 1969, Erbar 1983, van Heel 1984, Endress and Igersheim 1997); they usually enclose two ovules (occasionally only one in some carpels of a flower, Eames 1961, Tiagi 1964, Wilson 1976) with collateral placentation, positioned one on top of the other at anthesis (Baillon 1868, Blake 1972, Endress and Igersheim 1997). The ovules are anatropous, bitegmic and crassinucellar; however, only the lower ovule is fertile (Endress and Igersheim 1997). In contrast all core Laurales studied so far have a single ovule per carpel with median placentation (see Endress and Igersheim 1997).

Developmental studies on the gynoecium in Calycanthaceae are scarce and have focused on *Calycanthus*. Carpel development was studied by Erbar (1983), and van Heel (1984). Developmental studies of the ovules have also focused mostly on *Calycanthus*: Baillon (1868), Lignier (1892), and Endress (1972, only *Chimonanthus*). Several meiocytes were found to develop in the nucellus of *Calycanthus* (Jönsson 1881, Mathur 1968, Kamelina 1981) and *Chimonanthus* (Ly Thi Ba 1962, Endress 1972). Nothing is known about gynoecium development of *Idiospermum*, despite its extremely large seeds. Within Calycanthaceae, anthetic gynoecium features unique to *Idiospermum* include: presence of only one carpel (rarely up to five, Worboys 2003) and sessile and fleshy stigmas.

The morphology of *Idiospermum australiense* is distinctively different to that of the rest of the Calycanthaceae, especially in gynoecium morphology. Precise knowledge of gynoecium morphology and development of *Idiospermum australiense* will thus allow us to improve our ability to distinguish between possible plesiomorphies in Laurales and synapomorphies in

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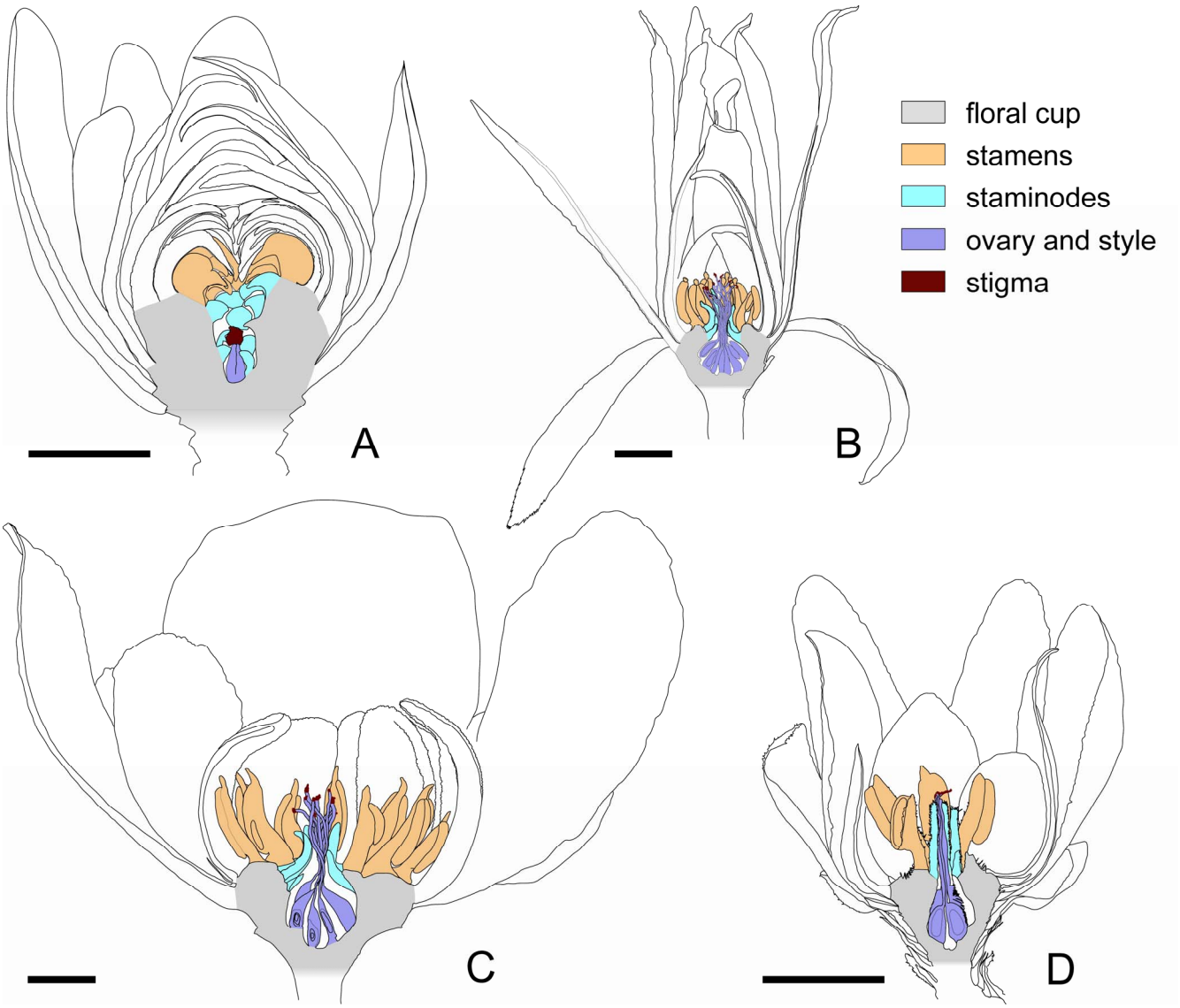

Fig. 1 Flower longitudinal sections at female phase of anthesis. A, *Idiospermum australiense*. B, *Calycanthus floridus*. C, *Sinocalycanthus chinensis*. D, *Chimonanthus praecox*. Scale bar = 5 mm.

Calycanthoideae. Features of interest include: presence or absence of a compitum, early carpel development, mode of carpel closure, stigma differentiation, placentation, ovule number, integument morphology and micropyle structure.

We studied and compared representatives of all four genera of Calycanthaceae in their gynoecium structure at anthesis (Fig. 1-12). Carpel development was comparatively studied for one representative of each subfamily: *Idiospermum australiense* for Idiospermoideae (Fig. 13), and *Calycanthus floridus* for Calycanthoideae (Fig. 14). As the morphological nature of the so-called staminodes has been disputed (stamen- or carpel-derived; Hiepko 1965), these organs are also included in this study. We discuss the implications of our findings on the morphological interpretations of fossil calycanthaceous flowers and on the evolution of gynoecium morphology in Laurales.

Material and Methods

The following species and collections were used for this study (materials collected from cultivated plants in the Botanic Garden of the University of Zurich are coded as "BGZ". Collections that are not attributed to a figure have been used for determination of organ number (number of carpels, number of staminodes, proportion of flowers with carpellodes, proportion of uniovulate carpels), or organ dimensions (stigma, style). For *Idiospermum* collections of populations North and South of Cairns are distinguished because populations South of Cairns tend to have more carpels per flower (Worboys 2003).

Idiospermum australiense (Diels) S. T. Blake: BPM Hyland 6242 (North of Daintree River, Queensland, Australia; population North of Cairns); YM Staedler S006-

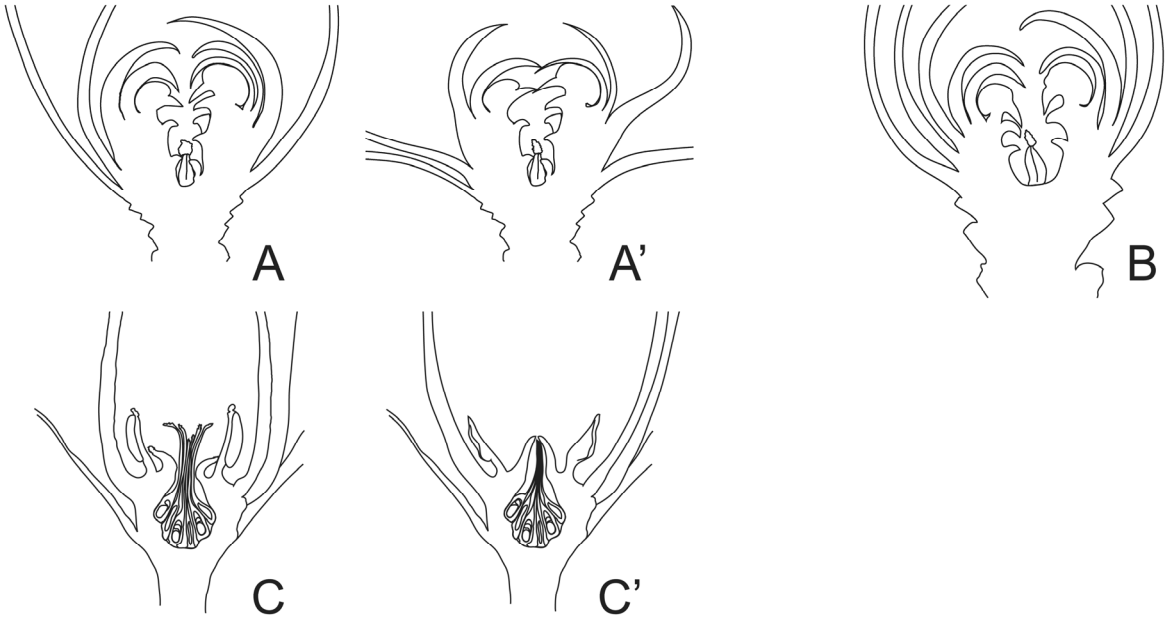

Fig. 2 Flower longitudinal sections showing anthesis process in Idiospermoideae and Calycanthoideae. A, A', B, *Idiospermum australiense*, population North of Cairns, A, female phase. A', male phase. B, population South of Cairns, female phase. C, C', *Calycanthus floridus*, C, female phase. C', male phase.

S006-27, S006-28 (Fig. 15D, 15D'), S006-29, S006-39, S006-57 (Fig. 15C, 15C'), S006-27 (Fig. 13E, 13E', 13F, 13F', 13F'', 13G, 13G', 15A, 15A', 15B, 15B', 15E, 15E'), S006-54 (Fig. 1A, 2A), S006-57 (Fig. 9A, 10A, 10A', 11A, 11A', 13H'') (CSIRO research plot, Daintree National Park, Queensland, Australia; population North of Cairns); PH Weston 004-10, 004-79, 004-245, 005-84, 005-85, 005-86, 005-87, 005-88, 005-89, 07-120, 004-245 (Fig. 13D, 13D'), 005-85 (Fig. 13A, 13A', 13B, 13B', 13C, 13C'), 005-88 (Fig. 3A), 005-89 (Fig. 13H, 13H'), 07-124-2 (Fig. 5, 4A, 12A) (Royal Botanic Gardens, Sydney, Australia; from population North of Cairns); SJ Worboys 395 (Fig. 2B) (Queensland, Australia; population South of Cairns).

Calycanthus floridus L. (one individual, BGZ): YM Staedler S004-42 (Fig. 14D, 14D'), S004-49 (Fig. 14F'', 14G, 14G', 14G''), S004-50 (Fig. 14E, 14E', 14E''), S004-50' (Fig. 14F, 14F'), S004-62 (determination of organ number, Fig. 6, 4B), S004-63 (Fig. 3B, 12B), S004-74 (Fig. 10B, B', 11B, 11B', 14H, 14H', 14H''), S004-90 (Fig. 9B), S007-67 (Fig. 14A, 14A', 14B, 14B'), S007-81 (Fig. 14C, 14C', 14D''), S007-90 (Fig. 1B, 2C, 2C'),

Sinocalycanthus chinensis (W.C. Cheng & S. Y. Chang) W. C. Cheng & S. Y. Chang (one individual, BGZ, individual n°2): YM Staedler S004-92 (determination of organ number, Fig. 9C, Fig. 10C, 10C', Fig. 11C, 11C'), S005-59 (Fig. 12C), S005-62 (determination of organ number, Fig. 7, Fig. 4C), S005-66 (Fig. 3C), S007-127 (Fig. 1C).

Chimonanthus praecox (L.) Link (one individual, BGZ): PK Endress 04-3 (determination of organ number, Fig. 8, Fig. 4D); YM Staedler S006-1 (Fig. 3D), S006-4 (fig. 1D), S006-8 (Fig. 9D, 10D, 10D', 11D, 11D', 12D).

Laurus nobilis L.: PK Endress 2654 (Fig. 16B) (cultivated, Ascona, Canton Ticino, Switzerland).

Organ number was determined by averaging numbers in three flowers of the same individual; organ dimensions were obtained by measuring dimensions on a typical organ, for three different flowers. Plant material was fixed and stored in 70% ethanol. Serial microtome sections were made after embedding in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate) (Igersheim and Cichocki 1996). The sections were stained with toluidine blue and ruthenium red. For scanning electron microscopy (SEM) studies, specimens were critical-point-dried, sputter-coated with gold and studied at 20 kV with a Hitachi S-4000 scanning electron microscope.

Results

Gynoecium structure at anthesis

Idiospermum australiense. Flowers have a pitcher-shaped floral cup with a thick wall; its inner space is deep and narrow, test tube-shaped in flowers of the populations North of Cairns (Fig. 1A, 2A, 2A'), and broad and beaker-shaped in the flowers of the populations South of Cairns (Fig. 2B). Most observations were made on flowers from the populations North of Cairns; for floral cup shape and carpel number, from both population groups North and South of Cairns. In our material the floral cup contains 0-2 carpels, and 13-21 staminodes (in all 3 opened buds of the population South of Cairns, 2 carpels were found, staminode number was not recorded). Carpels are borne at the bottom of the floral cup (Fig. 1A). The stigmas are

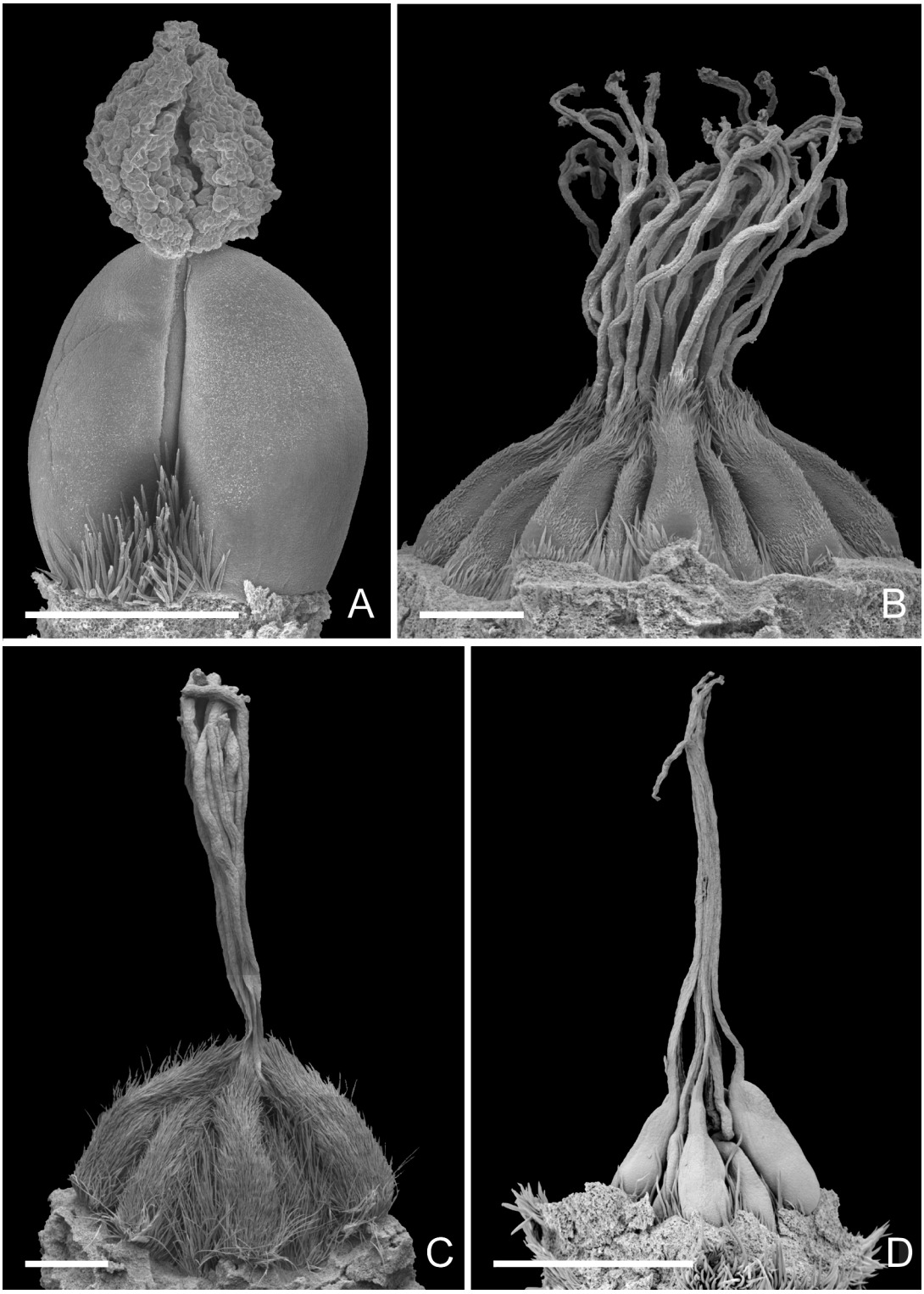

Fig. 3 Gynoecium (SEM micrographs). A, *Idiospermum australiense*. B, *Calycanthus floridus*. C, *Sinocalycanthus chinensis*. D, *Chimonanthus praecox*. Scale bar = 1 mm.

large, sessile, and papillate (about 0.8x0.4mm, Fig. 1A, 3A, 4A, 5A, 9A, 13H-H'), and do not protrude from the floral cup (Fig. 1A). When two carpels are present, the stigmas are postgenitally coherent and appear to form a compitum (Fig. 3A, 4A, 5A). Coherence of the stigmas is strong. They cannot be separated from each other without breaking off from the ovary. The staminodes line the entire inner wall of the floral cup (Fig. 1A).

Carpels are glabrous, except for the adaxial portion below the lower end of the ventral slit, which is covered by hairs (Fig. 13F-H). The stigma is bifacial (Fig. 4A, 5A). Most of the ovary is plicate (Fig. 5C-5E), but there is a distinct

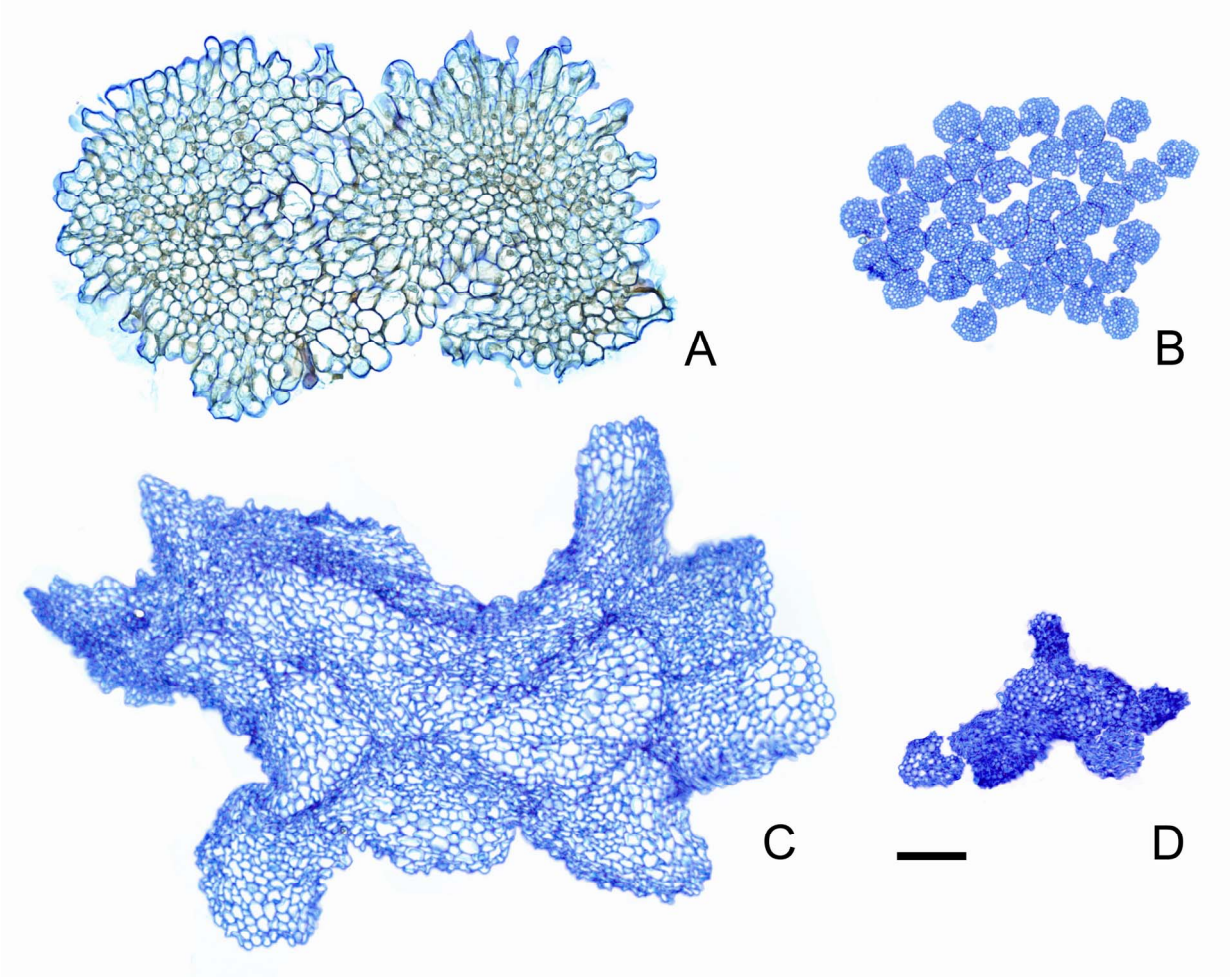

Fig. 4 Transverse sections of gynoecium at level of compitum. A, *Idiospermum australiense*. B, *Calycanthus floridus*. C, *Sinocalycanthus chinensis*. D, *Chimonanthus praecox*. Scale bar = 100 µm.

ascidiate base (Fig. 5F). At anthesis, the ascidiate zone is 240 (±45) µm long, which represents 17% of the ovary length. A short (20 µm) stipe is present in all five sectioned fertile carpels (Fig. 5G). The carpels have one dorsal and two lateral vascular bundles. The carpel wall is 10-12 cell layers thick at the level of the placenta, at mid-distance between the dorsal and lateral vascular bundles. The carpels contain usually two ovules (13 of the 18 studied carpels), but normally shaped carpels with one ovule, or no ovule at all, also occur (2 and 3 of the 18 studied carpels). The ovules have collateral placentation (Fig. 5E) at the base of the plicate zone, just above the beginning of the ascidiate zone. By curvature into different directions in early development, they come to lie one above the other (Fig. 9A).

The ovules are anatropous, bitegmic and crassinucellar. The lower ovule is ovoid (Fig. 10A) and 0.7-0.8mm long (Fig. 5C-5F). The outer integument is semiannular and lobed (Fig. 5F, 10A, 10A'). Usually the lobes of the outer integument are not appressed to each other, and the micropyle is formed by the inner integument (Fig. 5F carpel 1). Rarely one of the two lateral lobes of the outer integument is folded over the other and the micropyle is formed by both integuments (Fig. 12A). The rim of the outer integument is appressed against the bottom of the ovarial cavity. The rim of both integuments lacks hairs. At mid-length, the outer integument is 8-9 cell layers thick and the inner integument is 5-6 cell layers thick. The funicle is very short and relatively stout (Fig. 5E (carpel 1), 10A, 10A'). The ovule vascular bundle appears to ramify in the chalaza into 4 small bundles, which extend into the base of the outer integument (Fig. 12A). Ovules in uniovulate carpels are morphologically and topographically indistinguishable from the lower ovule in biovulate carpels.

The upper ovule is usually shorter, only two thirds of the length of the lower ovule (Fig. 9A) and not fully developed. It is hood-shaped (Fig. 11A, 11A'). The integuments do not cover the nucellus apex (Fig. 11A'); the nucellus is oriented downwards and the rim of the integuments faces the lower ovule and is contiguous with it (Fig. 9A). The funicle is long and slender (Fig. 11A), it is often detached from the placenta at anthesis. Most of the tissues of the upper ovule are shriveled (Fig. 11A, 11A').

Sterile carpel-like structures (carpellodes) are found in 12 of the 76 flowers with female reproductive structures studied. Carpellodes are usually columnar structures of

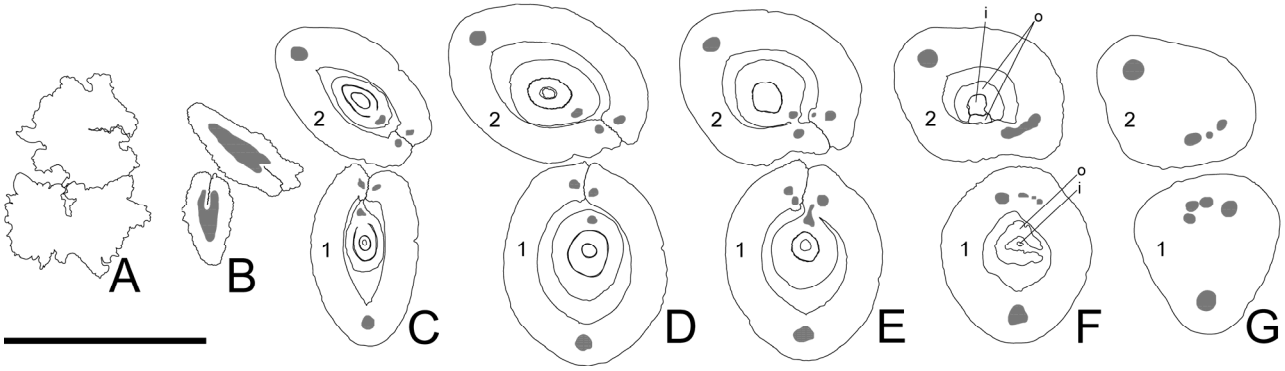

Fig. 5 *Idiospermum australiense*, transverse section series of anthetic bicarpellate gynoecium. Vasculature in grey. Carpels numbered. A, level of stigmas (compitum). B, level of styles. C, level of upper ovules. D, level of lower ovules. E, level of placentae. F, level of tip of lower ovules. G, level of stipes. o: outer integument, i: inner integument. Scale bar = 1 mm.

varying size, which often bear a stigma at anthesis (Fig. 15A-E'). A short ventral slit (Fig. 15A) and an inner space may be present (Fig.15A-B') or absent (Fig.15C-E'). Absence of postgenital fusion of the ventral slit, combined with the lack of a stigma was found in one case (Fig. 15B, B').

Calycanthus floridus. Flowers have a broad, urceolate floral cup (Fig. 1B, 2C, 2C') and contain 25-35 carpels, and 16-22 staminodes. Carpels are at the bottom and on the topographically lowest third of the wall of the floral cup (Fig. 1B). The styles are long and slender (4.7 mm long, 0.1 mm wide, Fig. 1B, 3B, 4B, 6A, 6A', 6B, 9B, 14H-14H''); they protrude from the floral cup, but are enclosed in the chamber formed by the inner tepals (Fig. 1B). The stigmas are short, papillate and secretory (ca. 0.2 mm long, Fig. 1B, 6A, 6A'). Secretion (stained red by ruthenium red) is found along the whole length of the styles. Most styles are postgenitally coherent and appear to form a vestigial compitum (Fig. 4B, 6B). The coherence of the styles is weak and separation of individual styles from the bundle of styles is easy; coherence does not seem to be resistant to preparation for scanning electron microscopy (Fig. 3B), but can be observed in transverse microtome sections (Fig. 4B, 6B). The staminodes are borne on the topographically upper third of the inner wall of the floral cup (Fig. 1B).

Carpels are covered with hairs, the hairs are longer at the base of the style and on the adaxial portion below the lower end of the ventral slit. The stigma is bifacial (Fig. 6A, 6A'). The style is plicate and the ventral slit is not postgenitally fused at this level (Fig. 4B, 6A, 6A'). Most of the ovary is also plicate, but with the ventral slit postgenitally fused (Fig. 6C carpels 5-29, 31; Fig. 6D; Fig. 6E carpel 32-35). There is only a short ascidiate base (Fig. 6E carpel 30, 33, Fig. 4F carpel 32, 34, 35). For inner carpels of the gynoecium, the ascidiate zone is 140 μm (±60 μm) long, which represents 8% of the ovary length. A short (ca. 100 μm) stipe is present in innermost carpels (Fig. 6F carpel 33); presence of a stipe is difficult to assess for peripheral carpels borne on the sides of the floral cup because their base is vertically and not horizontally oriented (Fig. 6C carpel 1-5). The carpels have one dorsal and two lateral vascular bundles. The carpel wall is 10-12 cell layers thick at the level of the placenta, at mid-distance between the dorsal and lateral vascular bundles. The carpels usually contain two ovules (98 of 100 carpels out of three flowers studied). Carpels with one ovule were also observed (2 of 100 studied carpels). A carpel devoid of ovules was observed once at the transition between staminodes and carpels. The ovules have collateral placentation (Fig. 6D carpel 31; Fig. 6D') at the base of the plicate zone, just above the beginning of the ascidiate zone. By curvature into different directions in early development, they come to lie one above the other (Fig. 9B, 14F'', 14G'', 14H'').

The ovules are anatropous, bitegmic and crassinucellar. The lower ovule is elongate-ovoid (Fig. 10B); it is 0.8-0.9mm long (Fig. 6C carpel 6, 8-18; Fig. 6D carpel 22, 24-33; Fig. 6E carpel 32, 33). The outer integument is semiannular and lobed (Fig. 6D, 6D''). One of the two lateral lobes of the outer integument is usually folded over the other. This "fold" is situated in the median plane of the ovule. Growth of the outer integument causes it to be moulded by the bottom of the ovarial cavity, such that the "fold" attains the form of a ridge (Fig. 10B, 10B'). In most ovules, the micropyle is formed by both integuments (Fig. 12B); in the innermost carpels of the gynoecium, the micropyle may be formed by the inner integument (carpel 34 Fig. 6E, 6F), or there may be no micropyle at all (carpel 35 Fig. 6E, 6F). A micropylar cavity is present between the outer and the inner integument and between the inner integument and the nucellus (Fig. 12B). Hairs extend from the rim of both integuments (Fig. 12B). At mid-length, the outer integument is 6-7 cell layers thick and the inner integument is 4 cell layers thick. The funicle is short and relatively stout (Fig. 6D', 10B, 12B). The ovule vascular bundle appears to ramify in the chalaza into 4 small bundles, which extend into the base of the outer integument (Fig. 12B). Ovules in uniovulate carpels are morphologically and topographically indistinguishable from lower ovules in biovulate carpels.

The upper ovule is usually shorter, only one half of the length of the lower ovule (Fig. 9B) and not fully developed. It is hood-shaped (Fig. 11B, 11B'). The integuments do not cover the nucellus apex (Fig. 11B, 11B'); the nucellus and

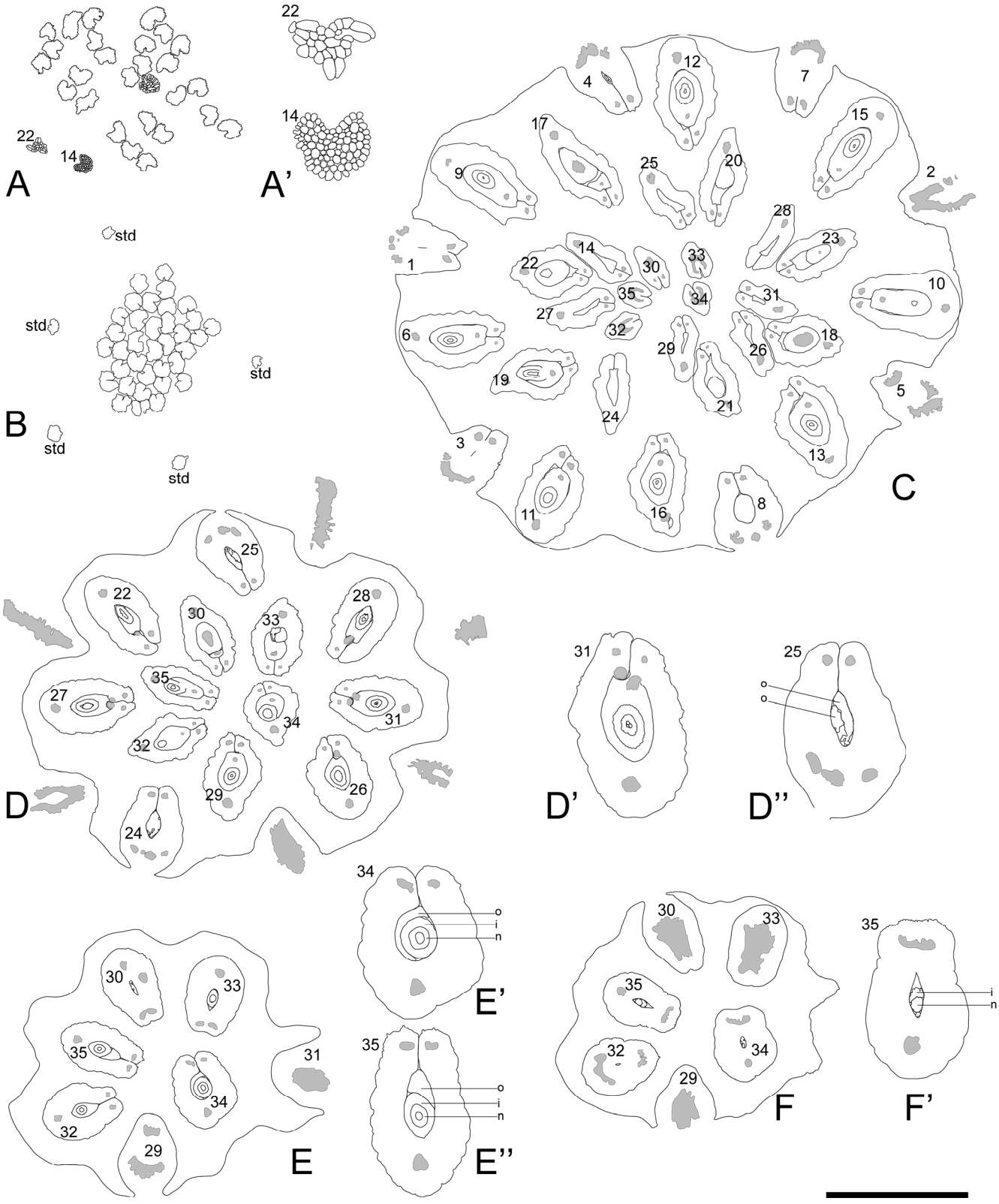

Fig. 6 *Calycanthus floridus*, transverse section series of anthetic gynoecium. Vasculature in grey. Carpels numbered in order of initiation. A, level of stigmas and styles. A', close-up of carpels 14 (style) and 22 (stigma). B, level of lower part of styles (compitum). C, level of middle part of ovaries. D, level of lower part of ovaries. D', close-up of carpel 31, level of placentae. D'', close-up of carpel 25, level of tip of lower ovule. E, level of ascidiate zone (carpel 30, 33) and tip of lower ovules of innermost carpels. E' close-up of carpel 34, level of the tip of the outer integument. E'', close-up of carpel 35, level of the tip of the outer integument. F, level of stipe (carpel 33) and ascidiate zone (carpels 32, 34, 35) of innermost carpels. F', close-up of carpel 35, level of the tip of the lower ovule. std: staminode, o: outer integument, i: inner integument, n: nucellus. Scale bar: Fig. 6A, 6B, 6C, 6D, 6E, 6F = 1 mm; Fig. 6A' = 250 μm; Fig. 6D', 6D'', 6E, 6E', 6E'', 6F' = 500 μm.

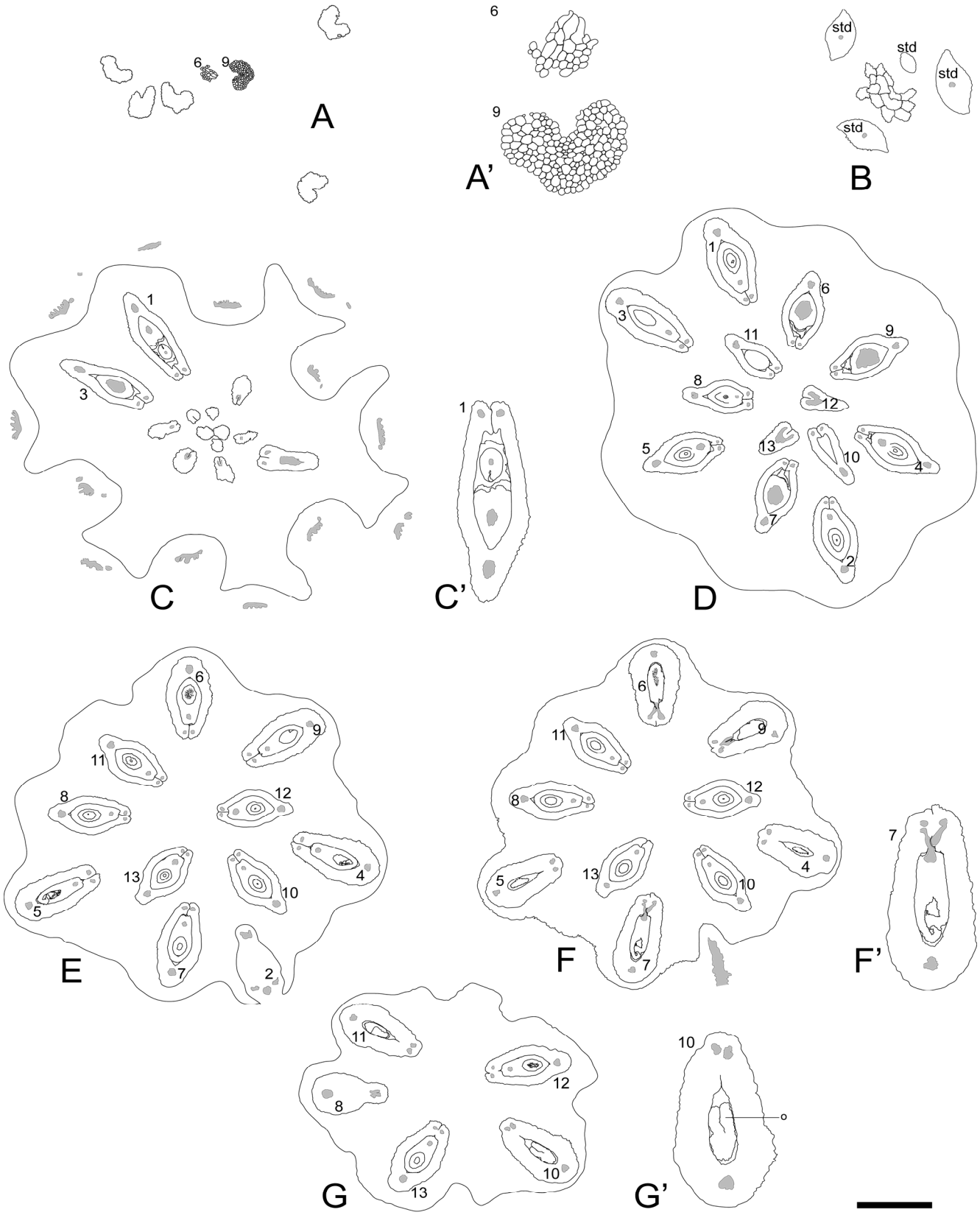

Fig. 7 *Sinocalycanthus chinensis*, transverse section series of anthetic gynoecium. Vasculature in grey. Carpels numbered in order of initiation. A, level of stigmas and styles. A', close-up of carpels 6 (stigma) and 9 (style). B, level of lower part of styles (compitum). C, level of lower part of styles and upper part of ovaries. C', close up of carpel 1 (upper ovule). D, level of upper part of ovaries. E, level of middle part of ovaries. F, level of lower part of ovaries. F', close-up of carpel 7 (placentation and outer integument fold). G, level of ascidiate zone (carpels 10,11) and stipe (carpel 8) of innermost carpels G', close-up of carpel 10. std: staminode, o: outer integument. Scale bar: Fig. 7A, 7B, 7C, 7D, 7E, 7F, 7G = 1 mm; Fig. 7A' = 250 μm; Fig. 7C', 7F', 7G' = 50

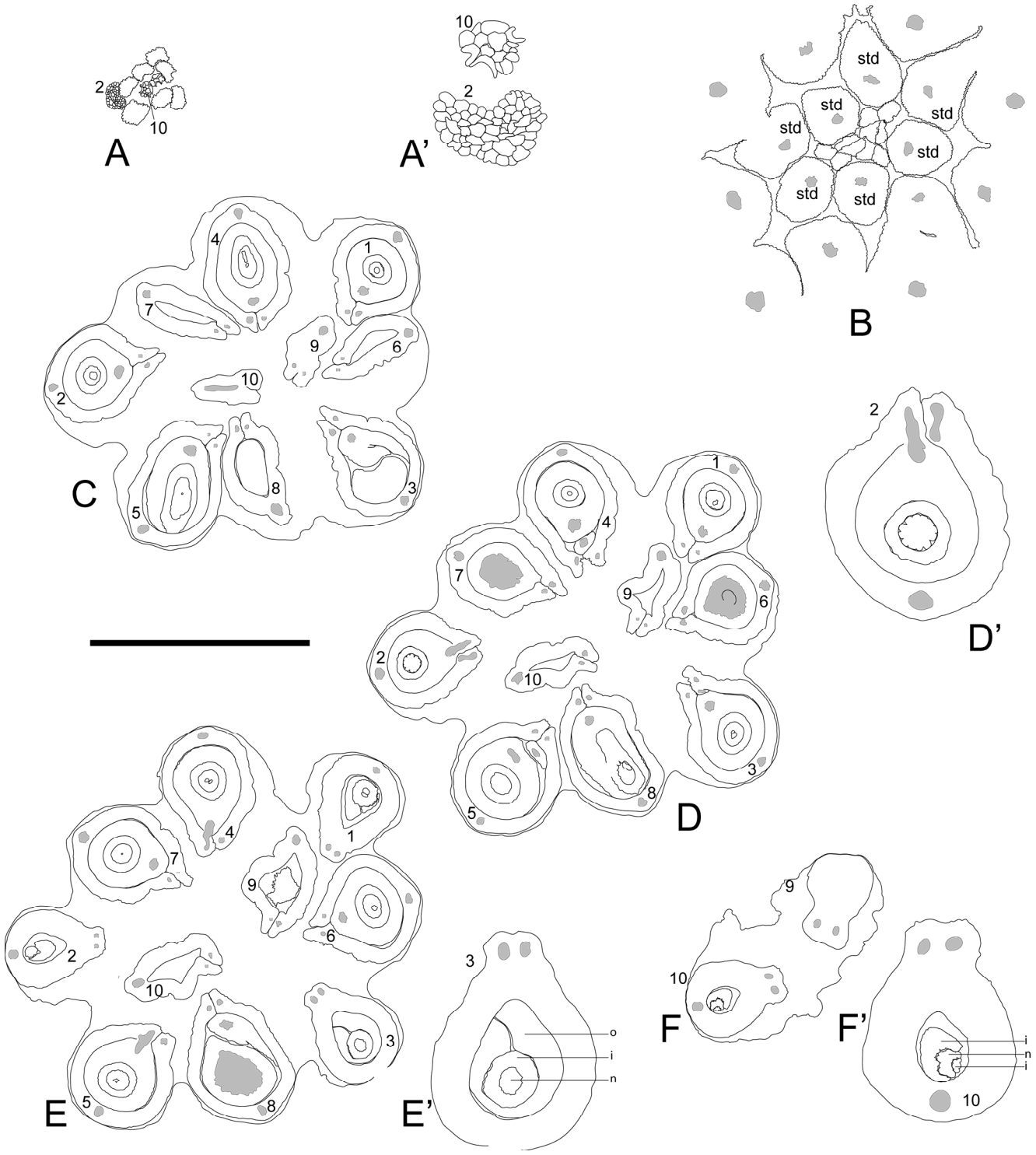

Fig. 8 *Chimonanthus praecox*, transverse section series of anthetic gynoecium. Vasculature in grey. Carpels numbered in order of initiation. A, level of stigmas and styles. A', close-up of carpels 2 (style) and 10 (stigma). B, level of lower part of styles (compitum). C, level of upper part of ovaries. D, level of middle part of ovaries. D', close-up of carpel 2, level of placentae. E, level of lower part of ovaries. E', close-up of carpel 3. F, level of ascidiate zone (carpel 10) and stipe (carpel 9) of innermost carpels. F', close-up of carpel 10 (protruding nucellus). std: staminode, o: outer integument, i: inner integument, n: nucellus. Scale bar: Fig. 8A, 8B, 8C, 8D, 8E, 8F = 1 mm; Fig. 8A' = 250 μm; Fig. 8D', 8E', 8F' = 500 μm.

the opening of the two integuments are oriented sidewards (Fig. 9B). The upper ovule lies on the lower one (Fig. 9B). The outer integument does not completely cover the inner integument in the contact zone between both ovules (Fig. 11B, 11B'); hence the inner integument is in contact with the lower ovule. The funicle is long and slender (Fig. 11B), it is often detached from the placenta at anthesis. The tissues of the upper ovule are usually strongly shriveled (Fig. 11B, 11B').

Fig. 9 Carpel, ovary opened. A, *Idiospermum australiense*. B, *Calycanthus floridus*. C, *Sinocalycanthus chinensis*. D, *Chimonanthus praecox*. Scale bar = 500 μm.

Aborted carpels are present in all six fruits studied. Conspicuous patches of aborted carpels were found in three of the six fruits. One or several sterile fruiting carpels were always found among the last initiated carpels of a gynoecium.

Sinocalycanthus chinensis. Flowers have a broad, urceolate to bowl-shaped floral cup (Fig. 1C) and contain 12-16 carpels, and 14-17 staminodes. Carpels are at the bottom and the topographically lowest third of the wall of the floral cup (Fig. 1C). The styles are long and slender (4.8 mm long, ca. 0.1 mm wide at the tip, 0.04 mm wide at the base, Fig. 1C, 3C, 4C, 7A, 7A', 9C); they protrude from the floral cup (Fig. 1C). The stigmas are short, and papillate (ca. 0.3mm long, Fig. 1C, 7A, 7A'). The basal portions of all the styles are covered with secretion (stained red by ruthenium red), they are postgenitally coherent, and appear to form a compitum (Fig. 3C, 4C, 7B); the tissue of the lower, coherent portion of the styles is small-celled and cytoplasm-rich (Fig.4C). Coherence of the styles is strong and separation of individual styles from the bundle of styles is difficult; coherence is resistant to preparation for scanning electron microscopy (Fig. 3C). The staminodes are borne on the topographically upper third of the inner wall of the floral cup (Fig. 1C).

The carpel indument is as in *C. floridus*. Stigma and style (Fig. 7A, 7A'), and ovary structure (Fig. 7C carpel 1,3; Fig. 7D carpel 1-11; Fig. 7E carpel 4-13; Fig. 7F carpel 6-13) are as in *C. floridus*. For inner carpels of the gynoecium, the ascidiate zone is 330 μm long, which represents 15% of the ovary length. A short (70 μm) stipe is present in innermost carpels (Fig. 7G carpel 8); presence of a stipe is difficult to assess for peripheral carpels borne on the sides of the floral cup because their base is vertically and not horizontally oriented. The carpels have one dorsal and two lateral vascular bundles. The carpel wall is 13 or 14 cell layers thick at the level of the placenta, at mid-distance between the dorsal and lateral vascular bundles. All 38 carpels out of 3 flowers studied contained two ovules. Placentation (Fig. 7F carpel 6, 7; Fig. 7F') and ovule direction (Fig. 9C) are as in *C. floridus*.

Ovule structure is as in *C. floridus*. The lower ovule (Fig. 10C) is 1.5-2 mm long (Fig. 7D carpel 1-9, 11; Fig. 7E carpel 4-13; Fig. 7F carpel 6-13; Fig. 7G carpel 12-13). The outer integument is as in *C. floridus* (Fig. 7G carpel 10; Fig. 7E carpel 5; Fig. 7F carpel 7; Fig. 7F', Fig. 10C, 10C'). Micropyle and micropylar cavity are as in *C. floridus* (Fig. 12C). At mid-length, the outer integument is 9 cell layers thick and the inner integument is 5-6 cell layers thick. Funicle shape and ovule vascularization are as in *C. floridus* (Fig. 7F', 10C, 12C).

The upper ovule is usually strongly reduced to a shriveled crust on the top of the lower ovule (Fig. 9C; Fig. 11C, 11C' show an ovule that is less reduced than usual, for structural clarity). It is hood-shaped (Fig. 11C, 11C') and faces the lower ovule. The integuments do not seem to cover the nucellus apex (Fig. 11C, 11C') and are contiguous with it (Fig. 9C). The outer integument occasionally grows along the surface of the lower ovule. The funicle is long and slender (Fig. 11C), it is detached from the placenta at

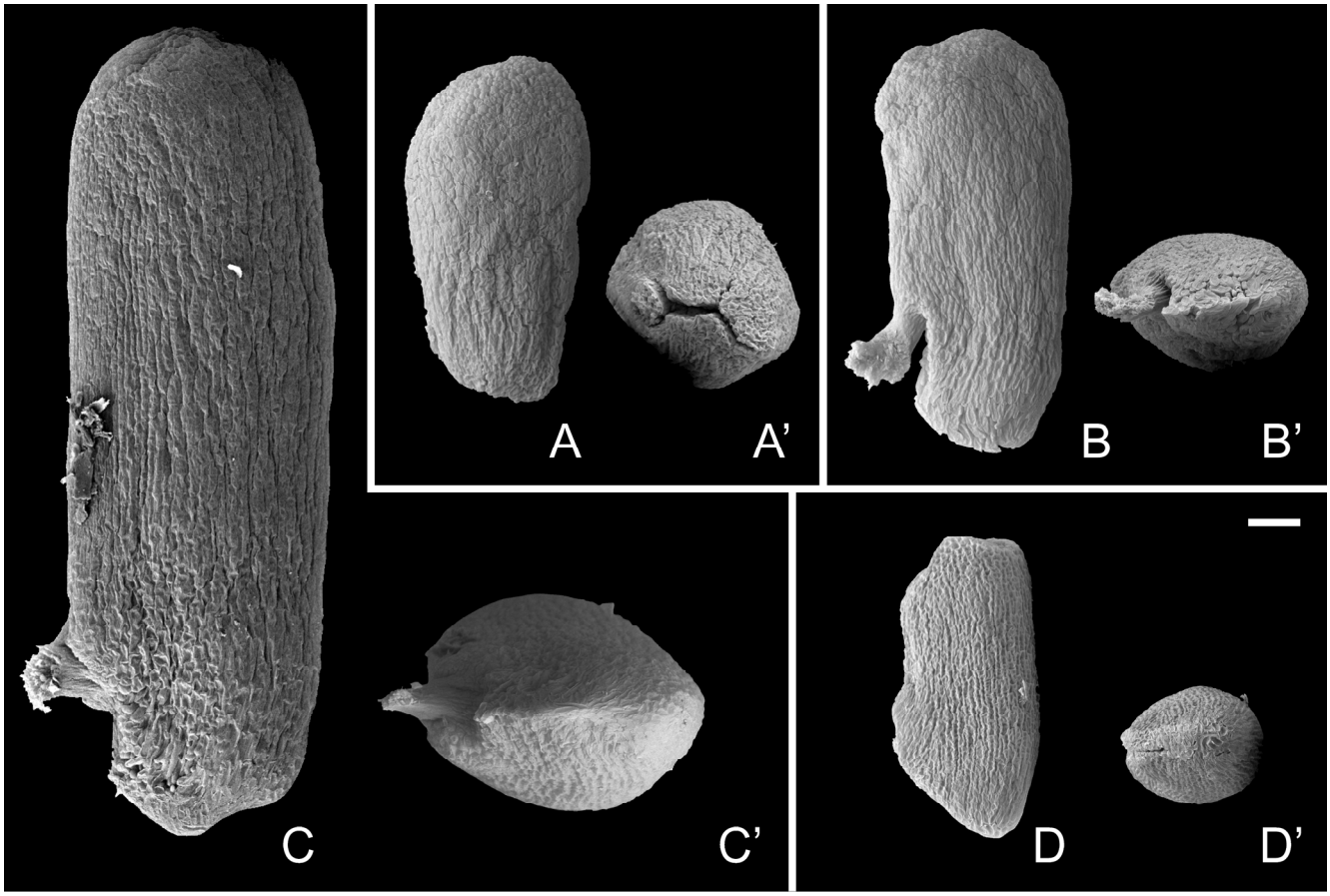

Fig. 10 Lower, fertile, ovule, micropylar and lateral view. A, A', *Idiospermum australiense*, A, lateral view. A', micropylar view. B, B', *Calycanthus floridus*, B, lateral view. B', micropylar view. C, C', *Sinocalycanthus chinensis*, C, lateral view. C', micropylar view. D, D', *Chimonanthus praecox*, D, lateral view. D', micropylar view. Scale bar = 100 μm.

anthesis. The tissues of the upper ovule are shriveled (Fig. 11C, 11C').

Aborted carpels are present in all nine fruits studied. A group of 4-5 aborted carpels on the topographically lower part of the floral cup was observed eight times. At least one sterile fruiting carpel was always found among the last initiated carpels of a gynoecium.

Chimonanthus praecox. Flowers have a narrow, urceolate floral cup (Fig. 1D) and contain 8-10 carpels and 8-12 staminodes. Carpels are at the bottom and on the topographically lowest third of the wall of the floral cup (Fig. 1D). The styles are long and slender (3.5 mm long, 80 μm wide, Fig. 1D, 3D, 4D, 8A, 8A', 8B, 9D), they protrude from the floral cup (Fig. 1D). The stigmas are short, and papillate (ca. 0.1 mm long, Fig. 1D, 8A, 8A'). The middle and lower portions of all the styles are covered with secretion (stained red by ruthenium red), they are postgenitally coherent, and appear to form a compitum (Fig. 3D, 4D, 8B); the tissue of the lower, coherent portion of the styles is small-celled and cytoplasm-rich (Fig. 4D). The coherence of the styles is weak and separation of individual styles from the bundle of styles is easy; coherence is only partially resistant to preparation for scanning electron microscopy (Fig. 3D), but can be observed in transverse sections (Fig. 4D, 8B). The staminodes are borne on the topographically upper fifth of the inner wall of the floral cup (Fig. 1D).

Carpels are glabrous, except for the adaxial portion below the lower end of ventral slit, which is covered by hairs. The stigma is bifacial (Fig. 8A, 8A'). The style is plicate and the ventral slit is not postgenitally fused at this level (Fig. 8A, 8A'). Most of the ovary is also plicate, but with the ventral slit postgenitally fused (Fig. 8C carpel 1-8; Fig. 8D; Fig. 8E carpel 4-10). There is only a short ascidiate base (Fig. 8E carpel 1-3; Fig. 8F carpel 10). For inner carpels of the gynoecium, the ascidiate zone is about 130 μm long, which represents 16% of the ovary length. A short (ca. 10 μm) stipe is present in all innermost carpels (Fig. 8F carpel 9); presence of a stipe is difficult to assess for peripheral carpels borne on the sides of the floral cup because their base is vertically and not horizontally oriented (Fig. 8E carpel 3). The carpels have one dorsal and two lateral vascular bundles. The carpel wall is 6 or 7 cell layers thick at the level of the placenta, at mid-distance between the dorsal and lateral vascular bundles. The carpels usually contain two ovules (75% of 28 studied carpels), carpels with one ovule were often observed (25% of 28 studied carpels). No carpel devoid of ovules was observed. The ovules have collateral placentation (Fig. 8D carpel 2; Fig. 8D') at the base of the plicate zone, just above the beginning of the ascidiate zone. By curvature into different

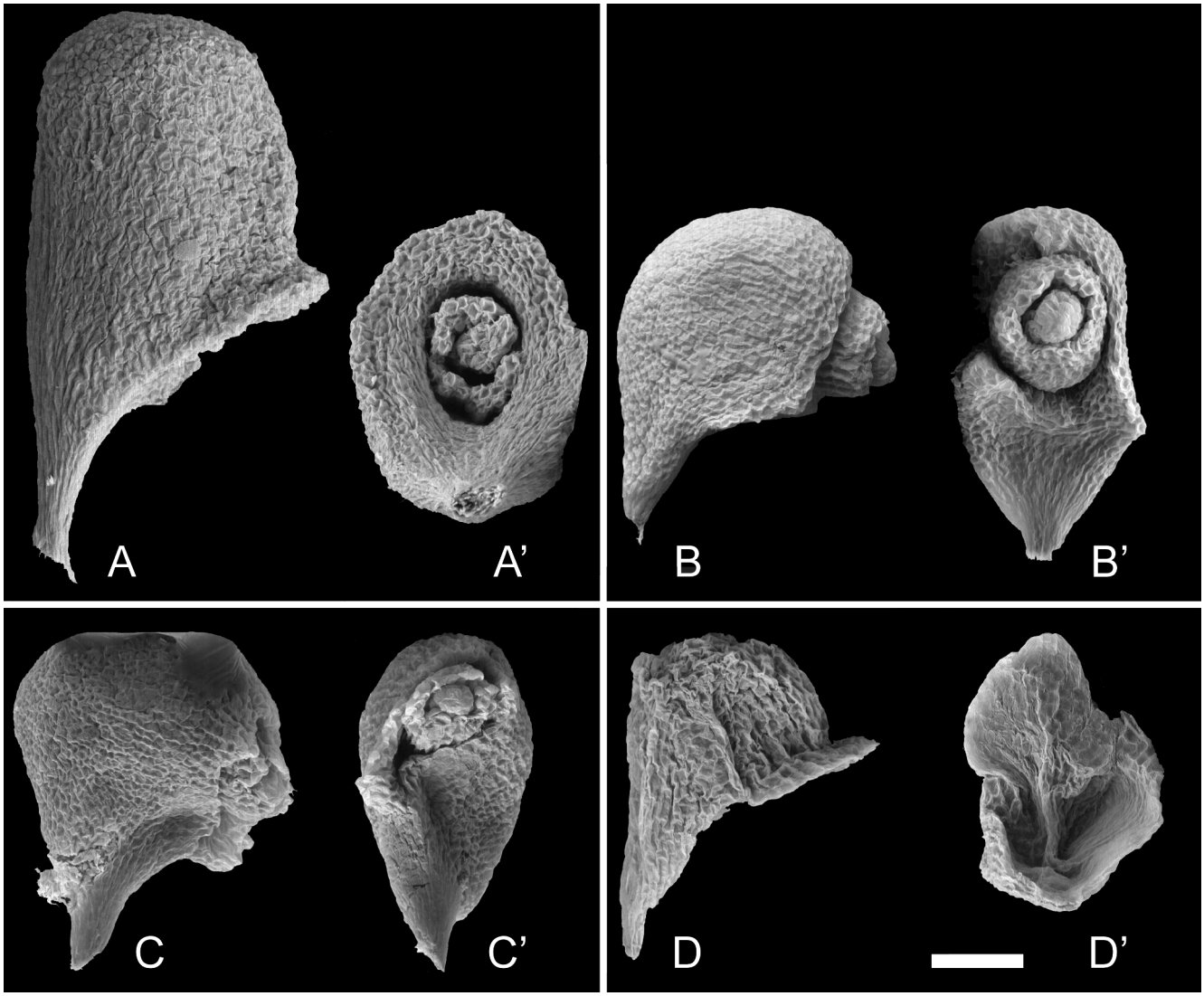

Fig. 11 Upper, sterile, ovule micropylar and lateral view. A, A', *Idiospermum australiense*, lateral view. A', micropylar view. B, B', *Calycanthus floridus*, lateral view. B', micropylar view. C, C', *Sinocalycanthus chinensis*, lateral view. C', micropylar view. D, D', *Chimonanthus praecox*, lateral view. D', micropylar view. Scale bar = 100 μm.

directions in early development, they come to lie one above the other (Fig. 9D).

The ovules are anatropous, bitegmic and crassinucellar. The lower ovule is ovoid (Fig. 10D); it is 0.5-0.9 mm long (Fig. 8C carpel 2; Fig. 8D carpel 2-5; Fig. 8E carpel 3-5). The outer integument is semiannular and lobed (Fig. 8E carpel 1, 3). One of the two lateral lobes of the outer integument is usually folded over the other. This "fold" is situated in the median plane of the ovule. Growth of the outer integument causes it to be moulded by the bottom of the ovarial cavity, such that the "fold" attains the form a ridge (Fig. 10D, 10D'). The inner integument protrudes at the abaxial extremity of this ridge and forms the micropyle (Fig. 12D). Very short hairs extend from the rim of both integuments. At mid-length, the outer integument is 6 cell layers thick and the inner integument is 4 cell layers thick. The funicle is short and relatively stout (Fig. 8D', 10D, 12D). The ovule vascular bundle appears to ramify in the chalaza into 4 small bundles, that extend into the base of the outer integument (Fig. 12D). Ovules in uniovulate carpels are morphologically and topographically indistinguishable from lower ovules in biovulate carpels (Fig. 8C carpel 1; Fig. 8D carpel 1, 6, 7; Fig. 8E carpel 1, 6, 7).

The upper ovule commonly shows all transitions in morphology from more or less well developed (in size about two thirds of the size of the lower ovule) to a crust of dry tissue on top of the lower ovule (Fig. 9D, 11D, 11D'; Fig. 11D, 11D' show a well-developed ovule for structural clarity). It is hood-shaped (Fig. 11D, 11D'). The integuments do not cover the nucellus apex (Fig. 11D, 11D'); the nucellus and the opening of the two integuments are oriented downwards (Fig. 9D) or sidewards (Fig. 11D). The outer integument occasionally grows along the surface of the lower ovule. The funicle is long and slender (Fig. 11D); it is often detached from the placenta at anthesis. The tissues of the upper ovule are commonly shriveled (Fig. 11D, 11D').

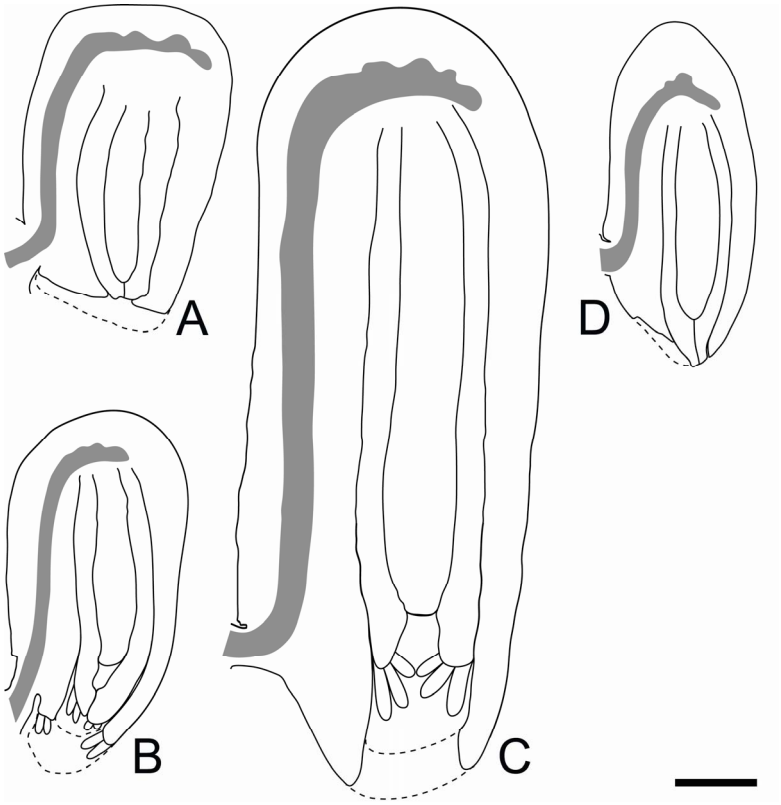

Fig. 12 Schematic longitudinal section of lower, fertile, ovule. A, *Idiospermum australiense*. B, *Calycanthus floridus*. C, *Sinocalycanthus chinensis*. D, *Chimonanthus praecox*. Thin dotted line: position reached by the folded lobe of the outer integument. Thick dotted line: possible micropyle. Scale bar = 200 μm.

Aborted carpels were always present in all the ten fruits studied. At least one sterile fruiting carpel is almost always present in the center of the gynoecium.

Gynoecium development

Idiospermum australiense. Carpels are initiated when the floral cup begins to develop and the stamens begin to elongate. The carpel(s) continue(s) the spiral phyllotaxis after the staminodes, with no apparent change in plastochron. Carpels differ from staminodes in being crescent-shaped, almost from the beginning. The two ends of the crescent representing the margins of the carpel are adaxially oriented (Fig. 13A, A'). The carpel thus exhibits conspicuous dorsiventrality almost from the beginning of its development. The dorsal side of the carpel elongates (cell rows in Fig. 13B), and the ends of the crescent (basal adaxial ends of the carpel) enlarge (Fig.13C'). Continuous growth of the dorsal side of the young carpel raises the primary margin, in lateral view to an angle of ca. 120° with the longitudinal axis of the flower (Fig. 13C). The basalmost part of the carpel becomes closed by "meristem fusion" over the ventral side. Thus a cross zone is now present (Fig. 13D, 13E). Above the cross zone, the two flanks of the carpels contact each other at first at the base, then gradually proceeding upwards (Fig. 13E). Ovule initiation appears to be concomitant with, or just subsequent to the beginning of carpel closure. A small bulge is initiated at the basal portion of each closing carpel flank, this bulge develops into an ovule. One of the two collaterally initiated ovules shows stronger basal curvature than the other, already during early development of the inner integument (see Fig. 13F'). Stigma differentiation appears to be concomitant with hair growth on the cross-zone (Fig. 13F-13F'). The stigma develops from the uppermost part of the carpel flanks; the stigma increases, first in width, then in length (Fig. 13G, 13G'). Elongation soon stops and the stigma becomes papillate and fleshy (Fig. 13H, 13H').

Calycanthus floridus. Carpels are initiated when the floral cup begins to develop and the stamens begin to elongate. The carpels continue the spiral phyllotaxis after the staminodes. Carpel primordia are approximately hemispherical (Fig. 14A, A'), they do not differ morphologically from staminode primordia. Strong apical growth in the adaxial region causes the adaxial surface to become parallel to the floral axis (Fig. 14B, 14B'). In lateral view, the young carpel resembles a mountain with a cliff on one side (adaxial side), and a smooth slope on the other (abaxial side). The young carpel continues to grow apically (Fig. 14C, C'), and two bulges (the initial margins) are initiated on each side of its basal adaxial surface, the carpel is then crescent-shaped in apical view. The basalmost part of the carpel becomes closed by "meristem fusion" over the ventral side. Thus a cross-zone is now present (Fig. 14D, 14E). Above the cross zone, the two flanks of the carpels contact each other from the base upwards (Fig. 14D, 14E). Ovule initiation appears to be concomitant with, or just subsequent to the beginning of

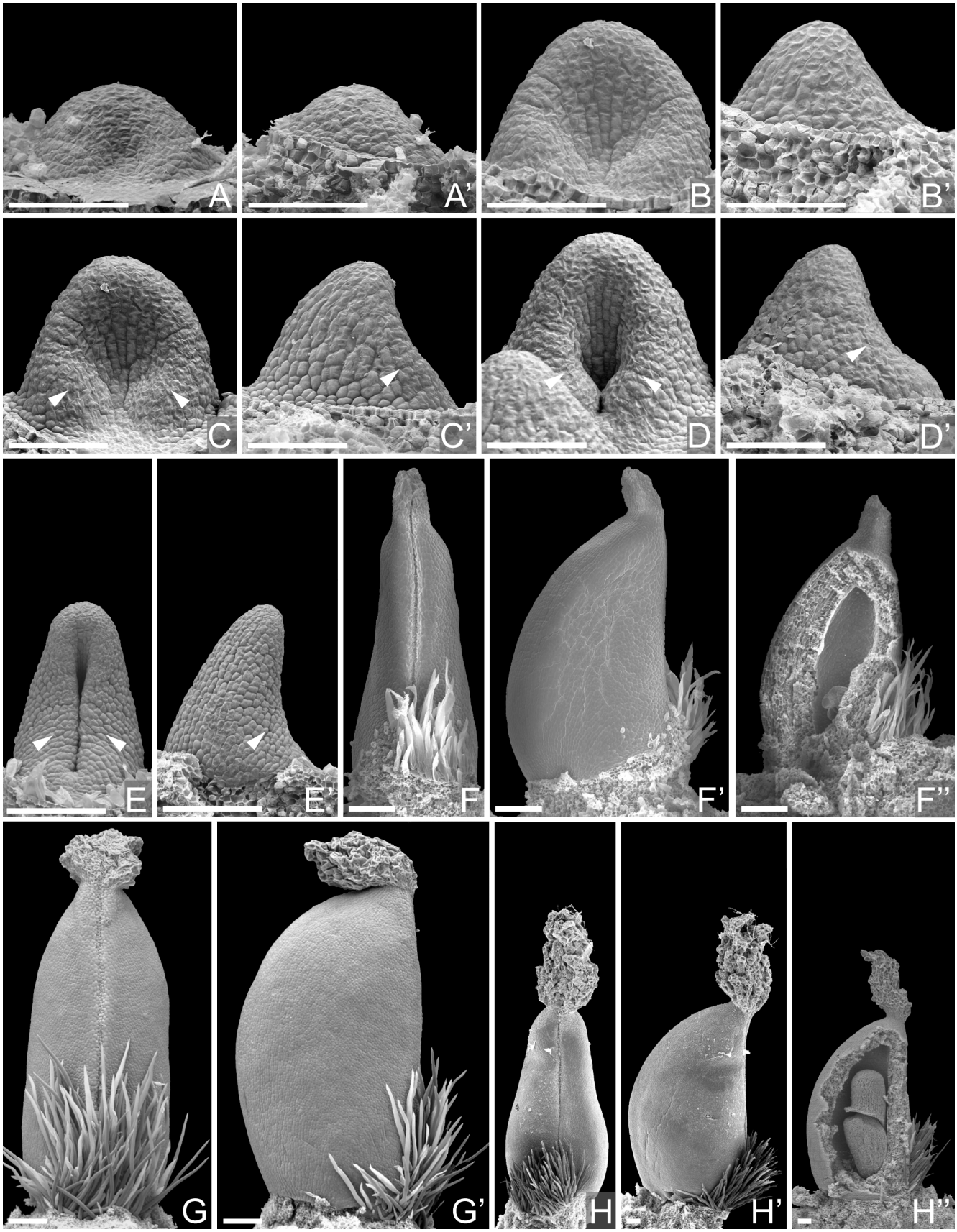

Fig. 13 Carpel development in *Idiospermum australiense*. A, A', carpel primordium, A, ventral view. A', lateral view. B, B', early carpel, B, ventral view. B', lateral view. C, C', early carpel, closure initiated, C, ventral view. C', lateral view. D, D', young carpel, early closure, D, ventral view. D', lateral view. E, E', young carpel, closure advanced, E, ventral view. E', lateral view. F, F', F'', carpel with stigma initiated, F, ventral view. F', side view. F'', ovary opened to show ovule with outer integument. G, G', carpel before anthesis, G, ventral view. G', lateral view. H, H', H'', anthetic carpel, H, ventral view. H', lateral view. H'', lateral view, ovary opened to show mature ovules. Arrowheads: direction of main growth. Scale bar = 100 μm.

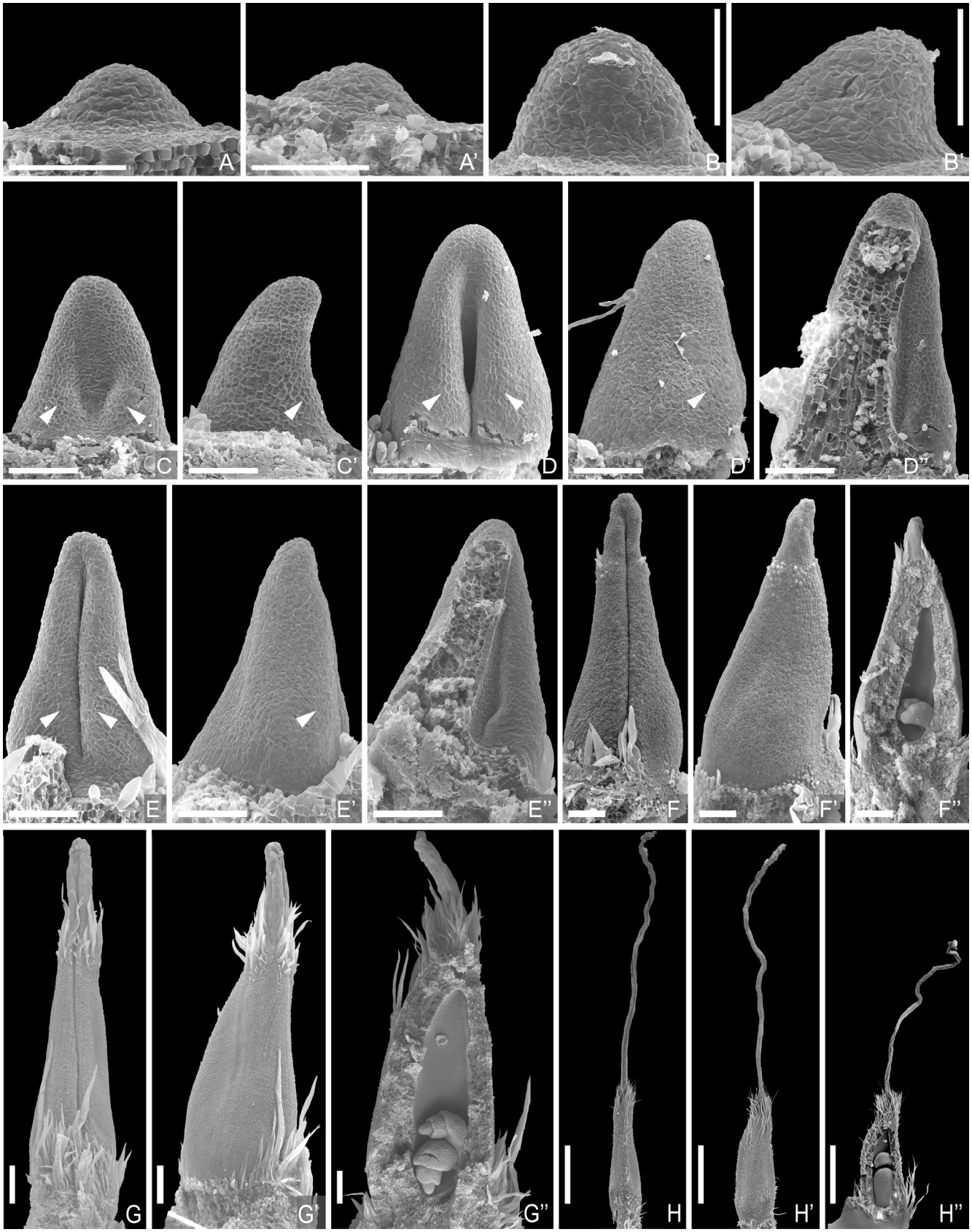

Fig. 14 Carpel development in *Calycanthus floridus*. A, A', carpel primordium, A, ventral view. A', lateral view. B, B', early carpel, B, ventral view. B', lateral view. C, C', early carpel, closure initiated, C, ventral view. C', lateral view. D, D', D'', young carpel, early closure, D, ventral view. D', lateral view. D'', opened. E, E', E'', young carpel, closure advanced, E, ventral view. E', lateral view. E'', opened to show lateral bulge with ovule initiation. F, F', F'', carpel with stigma and style initiated, F, ventral view. F', side view. F'', opened to show ovules with outer integument formed. G, G', G'', carpel before anthesis, G, ventral view. G', lateral view. G'', opened to show ovules one on top of the other. H, H', H'', anthetic carpel, H, ventral view. H', lateral view. H'', opened to show mature ovules. Arrowheads: direction of main growth. Scale bar: Fig. 14A-14G'' = 100 µm; Fig. 14H-14H'' = 1 mm.

carpel closure (Fig. 14D'', 14E''). A small bulge is initiated at the basal portion of each closing carpel flank (Fig. 14D, 14E), this bulge develops into an ovule (Fig. 14F''-14G''). One of the two collaterally initiated ovules shows stronger basal curvature than the other, already during early development of the inner integument (Fig. 14F''). Style and stigma differentiation appear to be concomitant with hair growth on the cross-zone (Fig. 14F-14G''). The style and stigma develop from the uppermost part of the carpel flanks (Fig. 14F-F''); style and stigma length appear to be increased by cell divisions (Fig. 14F-F''), then by cell elongation, the style becomes very long and slender (Fig. 14G-H''). Development of papillosity of the stigma seems to be concomitant or just subsequent to the arrest of style elongation (Fig. 14H-H'').

Discussion

Calycanthaceae: gynoecium structure at anthesis

In all Calycanthaceae studied, carpels possess a short stipe, a feature present in most "basal angiosperms" (Endress and Igersheim 2000a). Angiospermy is of type 4 (angiospermy by complete postgenital fusion; definition by Endress and Igersheim 2000a). The stigmas differ in size, shape and exposition in the two subfamilies: stout, fleshy, sessile and enclosed in the floral cup in *Idiospermum* (Blake 1972, this study), small, terminating an elongated, slender style, with the tips exerted from the floral cup in Calycanthoideae (Baillon 1868, Cheng and Chang 1963, 1964, this study). Despite the diversity in fruit size, vascularization of the carpels is similarly simple in both

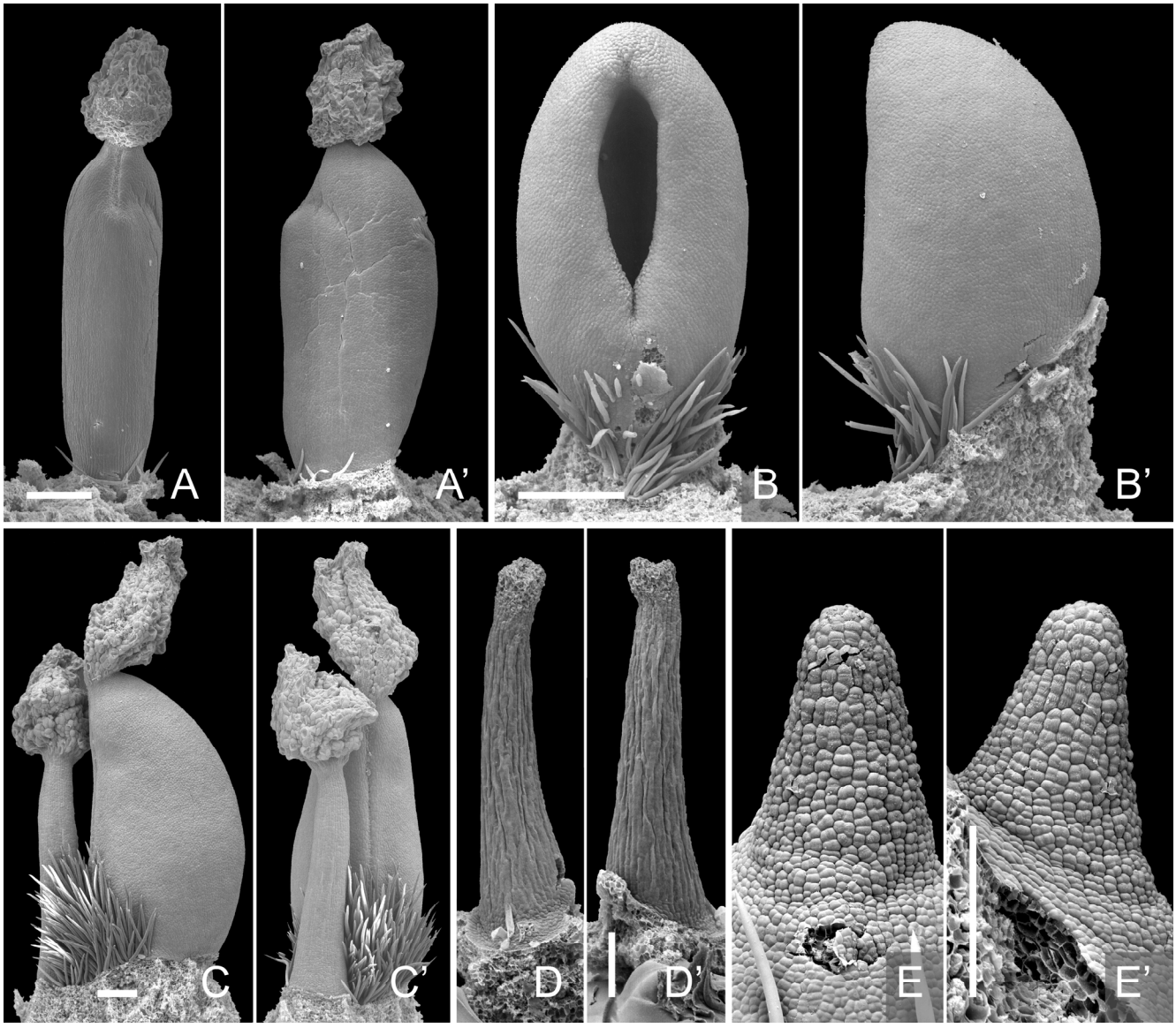

Fig. 15 Carpellodes in *Idiospermum australiense*. A, A', carpellode from anthetic flower with stigma and reduced ventral slit, A, ventral view. A', lateral view. B, B', carpellode from late bud without stigma and opened ventral slit, B, ventral view. B', lateral view. C, C', carpellode and carpel from anthetic flower, C, lateral view. C', ventral view. D, D', carpellode from late bud with stigma, D, adaxial view. D', lateral view. E, E', small carpellode from late bud, E, adaxial view. E', lateral view. Scale bar: Fig. 15A-15C = 200 μm; Fig. 15D-15E' = 100 μm.

subfamilies, including a dorsal and two lateral vascular bundles (see also Schaeppi 1953, Wilson 1976). Likewise, the thickness of the carpel wall is simply related to the size of the ovary at anthesis in both subfamilies, and not to carpel size at fruit maturity.

An extragynoecial compitum formed through postgenital coherence of carpels by secretion is present in all genera (Fig. 4A); however, there is variation in degree of postgenital coherence and in the area of the carpel that is involved in compitum formation. In *Calycanthus floridus*, they show loose coherence in small groups; the styles of the carpels of the center of the flower often show stronger coherence than those at the periphery (Fig. 4B). This difference may be related to the fact that the styles of the innermost carpels are not long enough for the stigmas to be exposed to the pollinators (Fig. 2C); therefore fertilization of the innermost carpels should require their stronger association with more peripheral carpels of the gynoecium. The patchy distribution of unfertilized carpels in fruits supports the hypothesis of the presence of partial compita between small groups of carpels. In *Sinocalycanthus chinensis* and *Chimonanthus praecox*, the lower portion of the styles show strong coherence in most flowers. In the zone of strong coherence the tissue is small-celled and cytoplasm-rich (Fig. 4C, 4D); such a zone may represent a plesiomorphic feature in Calycanthoideae.

Carpels commonly contain two ovules. If only one ovule is present, it is undistinguishable from the lower, fertile ovule of a biovulate carpel (see below). As the carpels at the center of the gynoecium, are initiated later than the others, their lower ovules may not be ready for fertilization by anthesis. This is suggested by (1) the observation of nucelli without a micropyle in the lower ovules of the innermost carpels (this study), and (2) the common occurence of sterile innermost carpels in the fruits of all Calycanthoideae (this study). In *Idiospermum* developmental delay seems unlikely to be the cause of the occurrence of solitary sterile carpels with strongly reduced ovules, or carpel-like structures with no ovule at all, sometimes with a stigma, but with no ventral slit (Fig. 15 A-E'). "Exhaustion" of the floral apex after the initiation of many organs could cause such columnar structures to arise, similar to the terminal structures found in the inflorescences of some alismatids (Sokoloff et al. 2006). In *Idiospermum* the most well developed sterile carpel-like structures bear a stigma; this indicates that stigma development is uncoupled from the initiation of ventral slit and ovules.

The size of the lower (fertile) ovule varies within the family and within species. *Idiospermum*, which has the largest embryos in angiosperms (Blake 1972), has unexpectedly small ovules (0.7-0.8 mm) compared to *Calycanthus* (0.8-0.9 mm) and *Sinocalycanthus* (1.5-2 mm), only *Chimonanthus* has smaller ovules (0.5-0.9 mm). Micropylar cavities between the outer and the inner integuments (previously reported by Endress and Igersheim 1997) and between the inner integument and the nucellus are present only in *Calycanthus* and *Sinocalycanthus* and may represent a synapomorphy for this clade. Protruding, uncovered nucelli are occasionally present in the innermost carpels of the gynoecium (*C. floridus*, *C. praecox*); however, a nucellar beak as described by Endress and Igersheim (1997) for lower ovules of *Idiospermum* was not observed in this study (if the definition given by Merino Sutter and Endress, 2006, is applied). In all taxa studied, the ovule vascular bundle appears to branch into four small bundles that extend into the base of the outer integument (Fig. 12A-D), as previously reported in young seeds of *Calycanthus* and *Chimonanthus* (Corner 1976) and anthetic ovules of *Idiospermum* (Endress and Igersheim 1997) (reviewed by Kimoto and Tobe 2001). In the upper (sterile) ovule, the time of onset of abortion is variable even at the species level. The integuments of the upper ovule do not cover the nucellus, but the outer integument may grow over the lower ovule to some extent (*Chimonanthus praecox*, *Sinocalycanthus chinensis*). The funicle of the upper ovule is slender and often detached from the placenta at anthesis. Detachment from the placenta could be caused by growth of the lower ovule, as the species with the largest fertile ovules (*S. chinensis*) has the most strongly reduced upper ovules. Conversely, farthest developed upper ovules are found in carpels with the smallest lower ovule (relative to the locule size) (*C. floridus*, *C. praecox*).

Calycanthaceae: gynoecium development

The most striking difference in carpel development between the sampled representatives of the two subfamilies of Calycanthaceae is the early crescent shape in *Idiospermum* in contrast to the consistently observed rounded shape of early carpels in *Calycanthus floridus*. This could represent another morphological difference between the two subfamilies, but could also be a sampling artifact. In *C. floridus*, the peripheral carpels are initiated before the inner ones. The peripheral carpels are already closed when the inner ones are at the primordium stage. It is thus easy to deduce the identity of the primordia of the inner carpels. However, in the andromonoecious *Idiospermum*, identification of the last initiated organ is difficult: it may be a carpel or a staminode; a primordium will then be interpreted as a young carpel only if it has a shape different of that of a staminode (i.e. crescent shape).

Ovule initiation is similar in both subfamilies. The initiation site is the proximal part of the flanks of the carpel, and initiation is approximately concomitant with carpel closure. This causes the proximal part of the flanks to grow more pronouncedly during early carpel closure; the carpel thus closes from the bottom upwards. A cross-zone is formed only after carpel closure.

Ovules and stigma are differentiated concomitantly in *C. floridus* and *I. australiense*. Although stigma morphology differs between subfamilies, this difference arises only late in development. After an initial elongation phase during which the stigmas of both species are similar in morphology (Fig. 13F-F''; Fig.14F-F''), the stigmas of *Idiospermum* broaden and become more fleshy, whereas the styles of *C. floridus* elongate to become filiform.

Ovule development is uniform in Calycanthaceae, including initial collateral placentation, rapid increase in curvature of one of the two ovules (about at the stage of inner integument initiation, Fig. 13F'', 14F''), late growth of the outer integument over the inner integument (Fig.

14G'', 14H''), and abortion of the upper ovule. The "nucellar beak" in *Idiospermum* (Endress and Igersheim 1997; see above) is reminiscent of the protruding nucelli observed in fertile ovules of the innermost carpels of *C. floridus*, which is probably due to precocious termination of the ovule development.

Morphological differences between subfamilies

Newly identified differences between the subfamilies include, (1) mode of formation of a compitum (stigma coherence in *Idiospermum*, style coherence in Calycanthoideae), (2) perhaps carpel primordium shape (hemispherical in *Calycanthus floridus*, early bifacial in *Idiospermum*), (3) outer integument morphology (lobes always growing over one another with a fold in Calycanthoideae, lobes mostly touching each other in *Idiospermum*), (4) epidermis differentiation of the rim of the integuments (hairs absent in *Idiospermum*, but present in Calycanthoideae). Surprisingly, at anthesis, in *Idiospermum* ovary and ovules are not larger, and the ovary wall is not thicker than in Calycanthoideae. However, the outer integument of *Idiospermum* is thicker (see also Endress and Igersheim 1997).

Previously documented reproductive morphological differences between the subfamilies include traits involving flower sexuality, perianth, androecium (incl. pollen, and staminodes), and notably, gynoecium (including fruit development). Perianth color change during anthesis is conspicuous in *Idiospermum* (Blake 1972, Staedler et al. 2007), but inconspicuous or absent in Calycanthoideae (Nicely 1965, Cheng and Chang 1963, Staedler et al. 2007). Stamens are sickle-shaped and staminodes are stout in *Idiospermum*, and elongated and narrowly triangular in Calycanthoideae (Blake 1972, Nicely 1965, Cheng and Chang 1963, Staedler et al. 2007). After anthesis, the floral cup is closed by movement of the stamens in *Idiospermum* (Fig. 2A, 2A') (Worboys 1998), and by movement of staminodes in Calycanthoideae (Fig. 2C, 2C') (Staedler et al. 2007). Pollen is monosulcate in *Idiospermum* (Blake 1972), but disulculate in Calycanthoideae (Ning et al. 1993, Sampson 2000). Stigmas are sessile and fleshy in *Idiospermum* (Blake 1972), but short and at the end of relatively long and slender styles in Calycanthoideae (Nicely 1965, Cheng and Chang 1963). In *Idiospermum*, at maturity all organ layers enclosing the embryo (including the enlarged floral cup, the carpel wall and the seed coat) decay: the dispersal unit is a naked, unusually large embryo dispersed by gravity (Blake 1972). In contrast, in Calycanthoideae, at maturity, the enlarged floral cup (which opens in some taxa and stays closed in others, Staedler et al. 2007) contains 1-25 fruitlets (personal observation), which are dispersed by rodents (van der Pijl 1982), or possibly by birds (Staedler et al. 2007). Water dispersal also seems likely in *Calycanthus* and *Sinocalycanthus* as both genera grow along creeks.

Comparison with core Laurales: gynoecium at anthesis

Stout and sessile stigmas, as in *Idiospermum*, are also found in some members of core Laurales, where they are either enclosed in the floral cup (most Monimiaceae; Perkins 1925, Endress 1980b) or exposed (*Hedycarya*, *Hortonia*, *Levieria* and *Xymalos* of Monimiaceae). However, slender, Calycanthoideae-like styles and stigmas that always protrude from the floral cup are found in other members of core Laurales (*Palmeria* of Monimiaceae, Atherospermataceae, Siparunaceae; Perkins 1925, Endress 1980b). This character combination could be plesiomorphic for the Siparunaceae-Atherospermataceae-Gomortegaceae clade, but seems to have evolved independently at least once in Monimiaceae (*Palmeria*, Renner 2004).

As in Calycanthaceae, angiospermy type 4 (angiospermy by complete postgenital fusion) occurs in all studied core Laurales (Endress and Igersheim 1997), except for taxa with a hyperstigma or a simple extragynoecial comitum, in which angiospermy type 1 (angiospermy by secretion) is present (*Tambourissa*, *Wilkiea*, *Kibara*, *Hennecartia, Faika*, *Hedycarya*, *Kibaropsis*; Endress 1979, 1980b, 1982, Endress and Lorence 1983, Philipson 1987, Endress and Igersheim 1997). Taxa with a hyperstigma, however, are restricted to some derived Monimiaceae (Renner 2004). Angiospermy type 4 (angiospermy by postgenital fusion) is thus likely to be ancestral in Laurales.

An extragynoecial compitum formed by contiguous carpel surfaces, like that found in Calycanthaceae, is present in all families of apocarpous pluricarpellate Laurales (Siparunaceae, Endress and Igersheim 1997, Renner et al. 1997; Atherospermataceae, *Daphnandra*, *Doryphora*, *Dryadodaphne*, Schodde 1969, Endress and Igersheim 1997; Monimiaceae, *Hedycarya*, *Kibaropsis*, *Palmeria*, Endress 1980b, Endress and Igersheim 1997). Similar observations were also made in the ANITA grade (*Amborella*, Endress and Igersheim 2000b; *Nymphaea*, Endress and Igersheim 2000a; *Austrobaileya*, Endress 1980c; *Illicium*, Thien et al. 1983, Endress and Igersheim 2000a; Schisandraceae, Igersheim and Endress 1997, Lyew et al. 2007). This character state could be a plesiomorphy for Angiospermae (sensu Cantino et al. 2007).

Unlike carpels of the Calycanthaceae with either two or one ovule(s) with lateral placentation, carpels of core Laurales always contain only one ovule with median placentation (Leinfellner 1966, 1968, 1969, Sampson 1969a, b, Endress 1972, 1980a, b, Endress and Igersheim 1997, Endress and Lorence 2004). The more profound difference between Calycanthaceae and core Laurales is thus ovule initiation site rather than ovule number.

Ovule morphology is diverse in core Laurales. However, a few character states present in Calycanthaceae are shared by most of the order: ovules anatropous (with the exception of *Gomortega*, orthotropous, Endress and Igersheim 1997, Heo et al. 2004), bitegmic (except for Siparunaceae, unitegmic, Heilborn 1931, Endress 1972, Renner et al. 1997, Kimoto and Tobe 2003) and crassinucellar (Endress and Igersheim 1997). The outer or the only integument, is semiannular or annular, with both character states observed in the same species in *Peumus* of Monimiaceae and *Siparuna* of Siparunaceae (Endress and Igersheim 1997). These traits (anatropous, bitegmic, crassinucellar, flexibility between annular and semiannular) may represent plesiomorphies for Laurales. In Calycanthaceae, the ovule vascular bundle branches in the chalaza and continues a

short distance into the base of the outer integument. In core Laurales, vascular bundles that branch in the chalaza are found in some Hernandiaceae and some Lauraceae; however, vascular bundles extending towards the rim of the outer integument were observed only in some *Hernandia* species (van Heel 1971, Heo and Tobe 1995, Endress and Igersheim 1997). Such a branching ovular bundle may represent an autapomorphy for the different groups considered (Calycanthaceae, Hernandiaceae p.p. and Lauraceae p.p.).

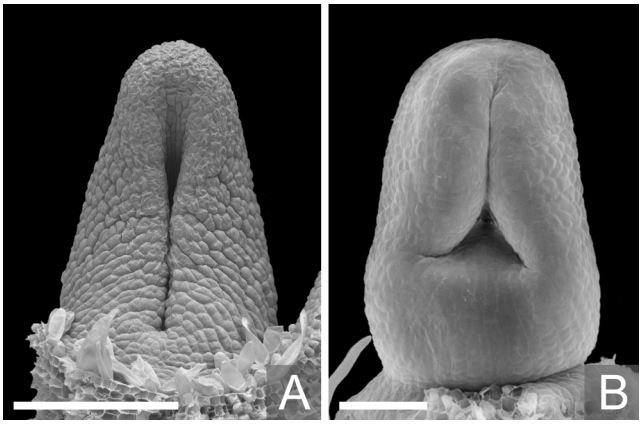

Fig. 16 Different carpel closure process in Calycanthaceae and Lauraceae, in ventral view. A, young carpel of *Idiospermum australiense*. B, young carpel of *Laurus nobilis*. Scale bar = 100 μm.

Comparison with core Laurales: gynoecium development

Comparative studies of carpel development in core Laurales are rare (Endress 1972 for a few Lauraceae and Monimiaceae s.l., 1980a for Monimiaceae s.l.). All studies are focused on only a few taxa: *Hedycarya arborea* and *Hortonia angustifolia* of Monimiaceae (Sampson 1969a, Endress 1980b), *Doryphora sassafras* and *Laurelia novae-zelandiae* of Atherospermataceae (Sampson 1969b, Endress 1972), *Hernandia nymphaeifolia* of Hernandiaceae (Endress and Lorence 2004), *Laurus nobilis, Cinnamomum camphora*, and *Persea americana* of Lauraceae (Endress 1972, Singh and Singh 1985, and Buzgo et al. 2007).

Young carpels in core Laurales differ from those in Calycanthaceae early in development. In Calycanthaceae, the ovules are initiated at the lower portion of the carpel flanks, approximately concomitantly with carpel closure, a cross zone is present only after carpel closure. In core Laurales however, the ovuliferous cross zone is initiated earlier, long before carpel closure begins (Fig. 16A, 16B).

In all Laurales studied ovule initiation is approximately concomitant with carpel closure, but the timing and localization of this initiation influences the mode of carpel closure. In Calycanthaceae, where the ovules are initiated from the basal part of the carpel flanks, the basal portion of the carpel flanks is bulkier and thus meets before the smaller distal portion; the flanks meet from the base upwards. In contrast, in core Laurales the large cross zone delays closure near the basis of the carpel, which proceeds from mid-length downwards. Furthermore the flanks initially do not meet at the very base of the carpel; there a secondary cross-zone is initiated to complete carpel closure (Sampson 1969b, Endress 1972, 1980a, b, 2006, Buzgo et al. 2007). Such a secondary cross-zone is not formed in Calycanthaceae.

Fossil taxa and evolutionary hypotheses

The fossil record of reproductive structures of Calycanthaceae comprises two taxa for which anthetic gynoecia are available: *Virginianthus calycanthoides* (Albian; Friis et al. 1994) and *Jerseyanthus calycanthoides* (Turonian; Crepet et al. 2005). *Virginianthus* has also been placed as potential sister to all other Laurales (including Calycanthaceae) (Crepet et al. 2005, Doyle and Endress 2007). Carpel number is 18-26 in the only available fossil of *Virginianthus* (Friis et al. 1994), and ca. 24 in *Jerseyanthus* (Crepet et al. 2005). In both fossils, carpel attachment and organization is similar to that of extant members of the family, although the attachment zone of the carpels of *Virginianthus* is broader than in extant Calycanthaceae. Both fossils appear to lack a compitum, but this could be a preservation artifact. Stigmas in *Virginianthus calycanthoides* appear small (as in Calycanthoideae) and sessile (as in Idiospermoideae). A large cell, which probably has a secretory function is found close to the stigma (Friis et al. 1994), a feature otherwise not found in Calycanthaceae. The extent of the ventral slit is difficult to assess because of poor preservation. In *Jerseyanthus*, the styles and stigma are conduplicate, slender and elongate. They are reminiscent of the developing style and stigma of carpels of Calycanthoideae just before anthesis (see Fig. 14G, 14G' for *Calycanthus floridus*); as in extant Calycanthaceae, the ventral slit runs down along most of the ovary. Morphology would suggest inclusion of *Jerseyanthus* in Calycanthoideae; however, as phylogenetic dating assesses the minimum age of the split between the two subfamilies to ca. 70 Mya (Zhou et al. 2006), whereas *Jerseyanthus* is estimated to be ca. 90 Mya old (Crepet et al. 2005), extant Calycanthoideae may have retained ancestral features of the family.

A zone of sterile organs is present between stamens and carpels in all Calycanthaceae, including both mentioned fossils (Nicely 1965, Cheng and Chang 1963, Blake 1972, Friis et al. 1994, Crepet et al. 2005). These organs are usually considered to be stamen-derived (Baillon 1868, Nicely 1965, Blake 1972, Chang and Chang 1963). Hiepko (1965) challenged this interpretation, hypothesizing that the "staminodes" were carpel-derived. This interpretation was based on observations of "staminode" and carpel primordia, which are indistinguishable, whereas a gap in the transition between "staminode" and stamen primordia was recognized (Hiepko 1965). Further support for this interpretation is provided by the occasional switch, along the ontogenetic spiral, from outermost carpels back to "staminodes" (Staedler et al. 2007). Postanthetic persistence of the "staminodes" would also favor a carpel origin. However, arguments in favor of a stamen-derived organ identity include: (1) occurrence of staminodes with a reduced pollen sac, especially in taxa with numerous stamens (*Calycanthus*, *Sinocalycanthus*, and *Idiospermum*), (2) Similar behavior of fertile stamens and staminodes during anthesis (Staedler et al. 2007), (3) Gene expression studies

on flowers normally bearing sterile organs between the stamens and the carpels: *Eupomatia* (Eupomatiaceae, Magnoliales, Kim et al. 2005), and *Aquilegia* (Ranunculaceae, Kramer et al. 2007), found stamen-like identity, (4) Difference between staminodes and true carpellodes occasionally found in *Idiospermum* (see above, Fig. 15): carpellode structure is variable, but when carpellodes are developed to a size comparable to that of a carpel, they almost always bear a stigma, they are often hollow, they may possess a (reduced) ventral slit and may even have the appearance of a normal carpel. Carpellodes are always positioned inside the gynoecium (not at its periphery); almost no morphological intergrading was observed between carpellodes and staminodes. Carpellodes have also been described in the fossil *Jerseyanthus calycanthoides* (presence of a ventral slit, inner cavity or stigma are not documented). But, in addition, the flowers also comprise staminodes that are morphologically distinct (petaloid) and positioned at the same place as staminodes in extant Calycanthoideae (Crepet et al. 2005). The arguments in favor of a stamen origin are more convincing than those in favor of a carpel origin, although developmental gene expression studies would be necessary to test this hypothesis more rigorously.

In some Magnoliales, inner staminodes appear to play a role in herkogamy, floral display and pollinator reward (Endress 1984). In Calycanthaceae, these inner staminodes may have a function in herkogamy (Staedler et al. 2007). A role in floral display could be assumed for the (petaloid) inner staminodes of *Jerseyanthus*, but not for extant Calycanthaceae. Pollinator reward is partially provided by staminodes in *Calycanthus* (Grant 1950), but this cannot be assumed for any other Calycanthaceae. The main function of staminodes in Calycanthaceae seems to be floral cup closure at the end of anthesis and during fruit development. This function is tightly associated with the situation of the fruiting carpels in a floral cup, which is not the case in Magnoliales. Interestingly, a coupling between floral display and pollinator reward seems to be present in Calycanthaceae, but these roles seem to be carried out by the inner series of perianth organs (Vogel 1998, Worboys and Jackes 2005, Staedler et al. 2007).

Calycanthaceae (extant and extinct) have lateral placentation throughout, independent of ovule number (this work, Friis et al. 1994, Crepet et al. 2005). This character state could be ancestral in Laurales. Arguments supporting this hypothesis include the presence of lateral placentation throughout the apocarpous members of Magnoliales (Igersheim and Endress 1997), the sister group of Laurales or the possible position of *Virginianthus* (with carpels with lateral placentation) as sister to the order (Crepet et al. 2005, Doyle and Endress 2007). Acquisition of median placentation has probably occurred on the branch leading to core Laurales.

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DIVERSITY AND LABILITY OF FLORAL PHYLLOTAXIS IN THE PLURICARPELLATE FAMILIES OF CORE LAURALES (GOMORTEGACEAE, ATHEROSPERMATACEAE, SIPARUNACEAE, MONIMIACEAE)

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Floral phyllotaxis of Laurales (Magnoliidae) is poorly and sometimes conflictingly documented, especially in the pluricarpellate families of the core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae). In this study four types of floral phyllotaxis were recovered: Fibonacci spiral, simple whorled (decussate), complex whorled, and irregular. Whorled and spiral phyllotaxis co-occur in all families except Gomortegaceae, and even vary within a species in some Mollinedioideae (Monimiaceae). Complex whorled floral phyllotaxis with two or more organs in a position where only one is expected and changes in merism are especially prominent in Atherospermataceae and Monimiaceae. The most elaborate complex whorled phyllotaxis pattern (leading to 8-merous whorls) is present in flowers with a flat floral base. Presence of a hyperstigma is correlated with double positions in the perianth. Flowers with low organ number commonly have simple whorled phyllotaxis, flowers with high organ number have complex whorled or irregular patterns. Spiral phyllotaxis occurs in flowers with broad range of organ numbers. Irregularities in organ sequence were found at the periphery of the gynoecium in some Atherospermataceae and Monimiaceae, involving staminodes, carpellodes and carpels. In Laurales, floral phyllotaxis diversity appears to have evolved from spiral phyllotaxis, independently in Atherospermataceae, Siparunaceae, and Monimiaceae.

Keywords: floral phyllotaxis, Atherospermataceae, Gomortegaceae, Monimiaceae, Siparunaceae, Laurales

Introduction

It has long been assumed that one of the general trends in angiosperm evolution is the evolution of whorled flowers from spiral ones (e.g., Takhtajan 1969; Kubitzki 1987; Cronquist 1988). This view was modified by Endress (1987) who, from the complex distribution of spiral and whorled flowers, hypothesized that spiral and whorled flowers coexisted in basal angiosperms and that the trend is not from spiral to whorled, but from lability between spiral and whorled to stabilization of whorled patterns. Whorled phyllotaxis allows synorganization and thus has a greater evolutionary potential than spiral phyllotaxis (Endress 1987, 2006). Phylogenetic studies indicate that in basal angiosperms, the evolutionary transition from a spiral to a whorled phyllotaxis or vice versa has occurred several times in the perianth and androecium (Endress and Doyle 2007, 2009; see also Zanis et al. 2003, perianth only; Ronse De Craene et al. 2003). Such transitions are, however, poorly understood. One of the groups in which such transitions took place is the Laurales (Endress and Doyle 2007, 2009; Ronse De Craene et al. 2003; Zanis et al. 2003).

Laurales (Magnoliidae sensu Cantino et al. 2007) comprise seven families. Calycanthaceae (9 species, Zhou et al. 2006) are sister to the rest of the order, the core Laurales (Renner 1998, 1999, 2004; Qiu et al. 1999, 2005) (fig. 1).

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The core Laurales consist of two subclades of three families each (Renner 2004): the clade containing Siparunaceae (53 spp.; Renner and Hausner 2005), Atherospermataceae (16 spp.; Renner et al. 2000), and Gomortegaceae (1 sp.; Kubitzki 1993a), and the clade containing Monimiaceae (ca. 270 spp.; Philipson 1993), Hernandiaceae (ca. 60 spp.; Kubitzki 1969, 1993b), and Lauraceae (2500-3500 spp.; Rohwer 1993). Siparunaceae are sister to Atherospermataceae plus Gomortegaceae (Renner 2004). Monimiaceae have an unsettled position either as sister to Lauraceae (Renner 1999, 2004), as sister to Hernandiaceae (Qiu et al. 1999, 2006), as sister to a clade comprising Hernandiaceae and Lauraceae (Doyle and Endress 2000; Chanderbali et al. 2001; Hilu et al. 2003), or the position of Hernandiaceae, Lauraceae and Monimiaceae is unresolved (Renner and Chanderbali 2000; Soltis et al. 2007). Monimiaceae are divided into two subfamilies, Monimioideae (*Peumus*, *Palmeria*, and *Monimia*) and Mollinedioideae (all other genera) (Renner 2004), with *Hortonia* as the basalmost genus.

Flowers of Laurales commonly have a floral cup (with the exception of some Lauraceae, Rohwer 1993). Unisexual flowers are common; in the pluricarpellate core Laurales, only few taxa have hermaphroditic flowers (Gomortegaceae, *Daphnandra*, *Doryphora*, and *Dryadodaphne* of Atherospermataceae, and *Hortonia* of Monimiaceae).

In Calycanthaceae, floral phyllotaxis is uniformly spiral in the Fibonacci mode (Staedler et al. 2007). In contrast, in unicarpellate families of core Laurales, spiral floral phyllotaxis is unknown; whorled patterns are predominant

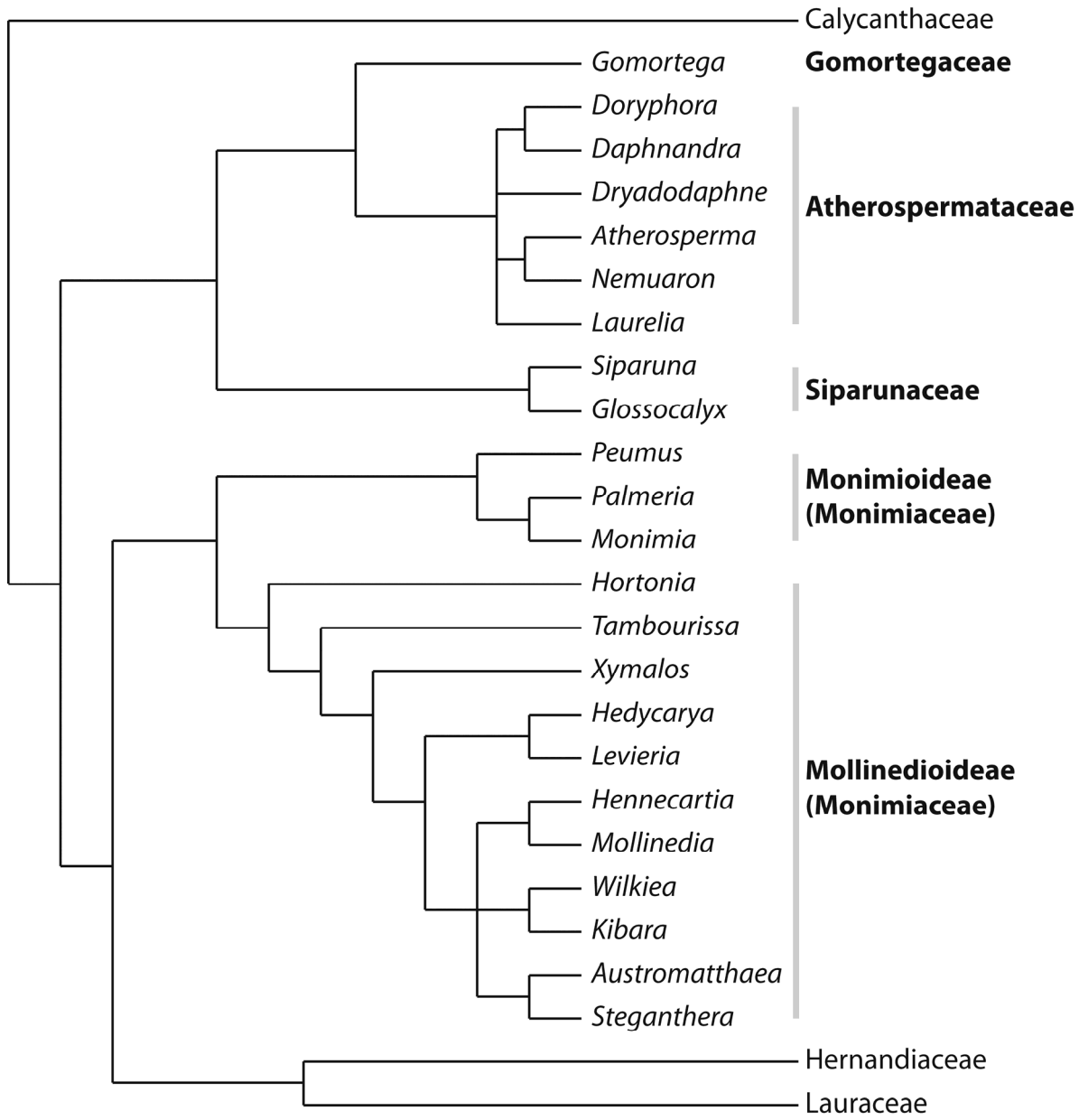

Fig. 1 Cladogram of Laurales (based on Renner 2004, and Soltis et al. 2007).

(Hernandiaceae; Kubitzki 1969; Endress and Lorence 2004; Lauraceae; Mez 1889; Singh and Singh 1985; Hyland 1989; Rohwer 1993; Buzgo et al. 2007). Irregular phyllotaxis has been reported in a few atepalous Lauraceae (Endress 1990).

In pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, and Monimiaceae), floral phyllotaxis appears to be diverse and labile. However, it is poorly documented in detail, especially for the androecium and even more so the gynoecium. Descriptions of the floral phyllotaxis of the sole species of Gomortegaceae, *Gomortega keule*, show conflicting results (summarized in Kubitzki 1993a). Atherospermataceae appear to be diverse (Schodde 1969), but published reports also show conflicting results. Baillon (1868) mentions spiral phyllotaxis for the whole flower of *Laurelia novae-zelandiae*, but his floral diagram shows a whorled perianth and spirally arranged stamens and carpels. For the same species, Sampson (1969b) mentions perianth phyllotaxis as either opposite for the two outer tepals and spiral for the other tepals or as entirely whorled, but with stamens and carpels spiral in both cases. In *Laurelia serrata*, completely tetramerous bisexual flowers were described (Stapf 1909). Schodde (1969) describes the phyllotaxis as whorled for perianth and androecium in bisexual flowers of *Atherosperma*, *Dryadodaphne* and *Laureliopsis* (*Laurelia*) *philippiana*, but spiral in the androecium of male flowers of *Atherosperma*; predominantly trimerous whorls in *Doryphora sassafras*, but tetramerous whorls in the perianth and more irregular pattern in the androecium of *Doryphora aromatica*; tri- and tetramerous whorls in *Nemuaron*; decussate and spiral phyllotaxis in *Daphnandra*; and obscure whorls in

Laurelia. Among Siparunaceae, in *Siparuna thecaphora*, phyllotaxis is decussate in most male flowers and spiral in carpels of female flowers (Endress 1972, 1980b), but it may also be irregular in other taxa of the family (Renner and Hausner 2005). In Monimioideae, floral phyllotaxis is not known in detail (but from preliminary observations, was assumed to be spiral in the perianth by Doyle and Endress 2000, and Endress and Doyle 2009). In Mollinedioideae it is documented for whole flowers only in very few taxa. *Hortonia* has a Fibonacci spiral pattern (Endress, 1980a). *Hedycarya arborea* has a whorled perianth, but stamen phyllotaxis is spiral or irregular, carpellodes are whorled and carpels spiral (Sampson, 1969a). For most species studied, data are limited to the perianth, which is often decussate, such as in species of *Austromatthaea, Kairoa,*

Kibara, *Mollinedia, Steganthera, Tambourissa*, and *Wilkiea* (Endress 1979a, 1980b; Philipson 1980, 1985). Thus from the literature, floral phyllotaxis in Atherospermataceae and Monimiaceae appears unusually diverse and unstable.

The present work is a comparative study of floral phyllotaxis in all four pluricarpellate families of the core Laurales. A number of taxa are studied for the first time, with the aim of resolving inconsistencies in earlier descriptions. Patterns and conditions of the unusual diversity and variability of floral phyllotaxis in the core Laurales are explored, such as different organ numbers, floral structure (shape, presence of hyperstigma), and gender in unisexual flowers (figs. 2-22). Finally, the results are discussed in an evolutionary context.

Material and Methods

Collection data

The following collections were used for this study (PKE = Peter K. Endress; S = Yannick M. Staedler; BGZ = cultivated in the Botanical Garden of the University of Zurich; cursory = cursorily studied flowers).

Gomortegaceae

Gomortega nitida Ruiz et Pav.; T. Stuessy *et al.* 6698, Chile (fig. 4*A*-4*D*)

Atherospermataceae

Atherosperma moschatum Labill.; PKE 2672, male flowers; Royal Botanical Gardens Kew, U.K.

Daphnandra micrantha Benth.; PKE 4169 (fig. 5*D*, 5*E*); PKE 4327 terminal flower; PKE 4350 (figs. 5*F*, 5*G*, 22*B*); Queensland, Australia.

Daphnandra repandula F. Muell.; PKE 4222 (fig. 5*A*-5*C*); PKE 4243 (fig. 22*A*); S006-32.1; Queensland, Australia

Doryphora aromatica (F. M. Bailey) L.S. Sm.; S 006-32 (fig. 6*A*-6*C*); B.P.M. Hyland 8610; Queensland, Australia.

Doryphora sassafras Endl.; PKE 2671; Royal Botanical Gardens Kew, U.K.

Dryadodaphne trachyphloia Schodde (ined. Schodde, 1969); B.P.M. Hyland 8261 (fig. 7*A*-7*C*); A. Ford 4791; Queensland, Australia.

Laurelia sempervirens (Ruiz et Pav.) Tul.; PKE 916 male; Royal Botanical Gardens Kew, U.K.

Siparunaceae

Glossocalyx longicuspis Benth.; W. de Wilde 1241 (*Z*) male; Cameroon.

Siparuna thecaphora Hemsl.; PKE 1096 male (fig. 8*H*-8*J*), Honduras; PKE 1202 male; PKE 1301 female (fig. 8*K*-8*M*); PKE 1203 female; Guatemala.

Monimiaceae

Monimioideae

Palmeria gracilis Perkins; PKE 4084 male (fig. 10*A*-10*E*); PKE 4085 female (fig. 10*F*, 10*G*); Papua New Guinea.

Peumus boldus Molina; V. Cassels s.n., male and female; Chile.

Mollinedioideae

Austromatthaea elegans L.S.Sm.; PKE 4196 male (fig. 19*A*, 19*B*); PKE 9030 male and female; Queensland, Australia.

Hedycarya angustifolia A.Cunn.; L. Adams 2473 male (fig. 14*A*); New South Wales, Australia; R. Schodde 2462 female (fig. 14*B*-14*E*) Australian Capital Territory, Australia.

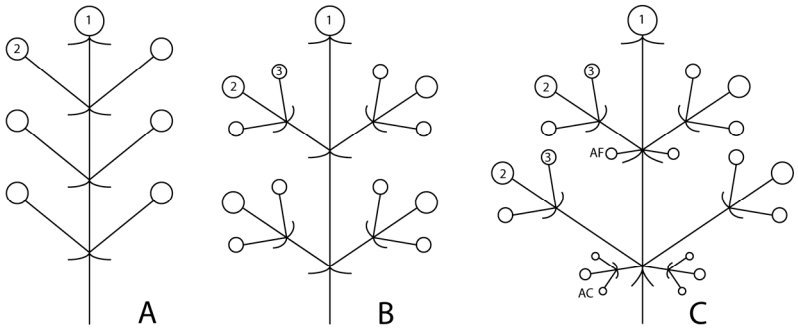

Fig. 2 Inflorescences. A, botryoid. B, thyrsoid. C, thyrsoid with accessory single flowers, and accessory cymes. Number = branching order. AF = accessory flower. AC = accessory cyme.

Kibara coriacea (Blume) Tul.; A.D.E. Elmer 20669 Borneo (Z) male (fig. 16*A*, 16*B*); PKE 9325 male; Botanical Garden Bogor, Java, Indonesia.
Kibara macrophylla (R.Cunn.) Benth.; PKE 9303 female; Botanical Garden Bogor, Java, Indonesia.
Levieria acuminata (F.Muell.) Perkins; S 006-75A male; S 006-75B female; Queensland, Australia.
Steganthera ilicifolia A.C.Sm.; PKE 4070 male (fig. 20*A*, 20*B*); PKE 4051 male; PKE 4071 male; PKE 4074 male; PKE 4126 female (fig. 20*C*, 20*D*); Papua New Guinea.
Tambourissa comorensis Lorence; D.H. Lorence 2870 female, Grande Comore Island.
Tambourissa ficus (Tul.) A. DC.; D.H. Lorence 2162 female, Mauritius.
Tambourissa purpurea A.DC.; PKE 03-3 male and female (figs. 11, 12); S08-01 male and female; Botanical Garden of the University of Zurich (original collection W. Rauh 138, Madagascar).
Wilkiea angustifolia (Bailey) Perkins; B. Gray 1913 male; Queensland, Australia.
Wilkiea cf. angustifolia (Bailey) Perkins; PKE 9216 female; Queensland, Australia.
Wilkiea huegeliana (Tul.) A. DC.; PKE 4398 male (fig. 18*A*-18*C*, 18*D*-18*F*); PKE 4182 female (fig. 18*G*-18*K*); PKE 4313 female; PKE 4330 female (fig. 18*L*-18*O*); PKE 4331 female; Queensland, Australia.
Wilkiea longipes (Benth.) Whiffin et Foreman; B.P.M. Hyland 11669 female; Queensland, Australia.
Xymalos monospora Baill.; B.M. Browning 37 male; Zimbabwe; R. Dümmer 814 (Z) female; Uganda.

Inflorescences or flowers were fixed in FAA or 70% ethanol and stored in 70% ethanol. Plant material embedded in paraplast was sectioned and stained with safranin and astra blue. Plant material embedded in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate) (Igersheim and Cichocki 1996) was sectioned and stained with toluoidine blue and ruthenium red. Sectioned herbarium material (all from the herbarium of the University of Zurich (Z)) was first expanded in sodium sulfosuccinate solution (Erbar 1995). The studied material and microtome slides are stored in the Institute of Systematic Botany of the University of Zurich. Additional unsectioned flowers were cursorily studied with the stereomicroscope.

Glossary

- *Accessory cyme*: a cyme borne in the axil of the same subtending bract as another lateral part of an inflorescence (fig. 2*C*).
- *Accessory flower*: a flower borne in the axil of the same subtending bract as another lateral part of an inflorescence (fig. 2*C*).
- *Botryoid*: determinate raceme (fig. 2*A*).
- *Compitum*: shared pollen tube transmitting tract of all carpels of a flower.
- *Hyperstigma*: receptive area for pollen outside the gynoecium, in some Mollinedioideae on the narrow floral pore formed by the floral cup and the reduced tepals.
- *Orthostichies*: radial straight lines connecting adjacent floral organs. Orthostichies are characteristic for whorled phyllotaxis.
- *Parastichies*: spiral lines from periphery to center connecting adjacent floral organs. Parastichies are characteristic for all regular phyllotaxis patterns (spiral and whorled). Several sets of parastichies running to the left or to the right are always present. If the parastichy sets of opposite directions have parastichies of different steepness the phyllotaxis is spiral, if the steepness is the same the phyllotaxis is whorled (Endress 2006).

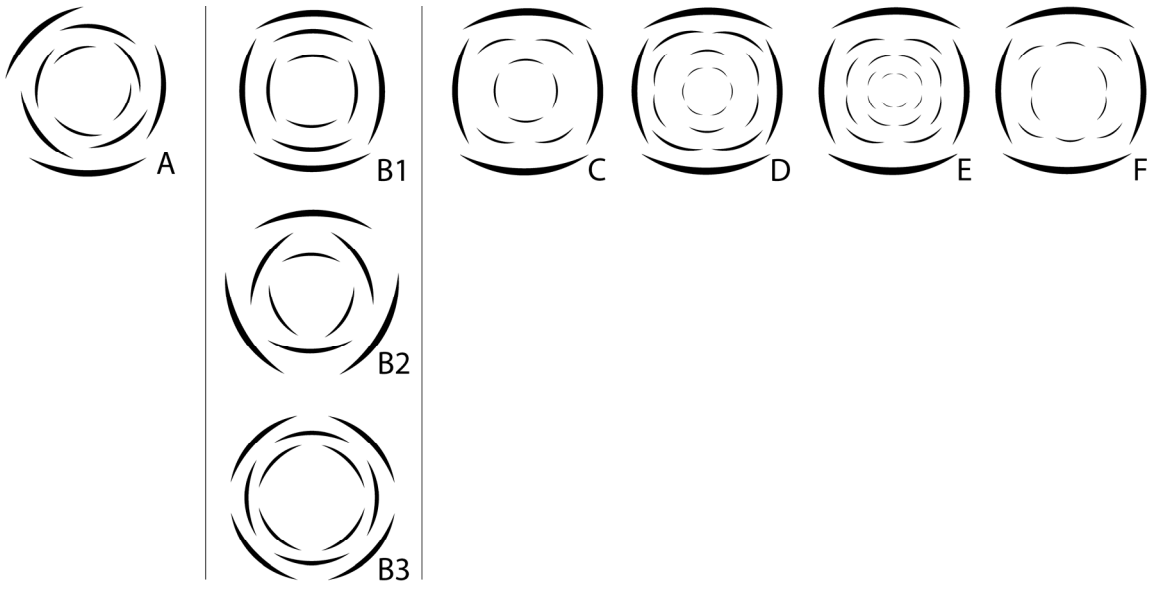

Fig. 3 Phyllotaxis patterns. A, Fibonacci spiral. B1-B3, simple whorled. B1, decussate. B2, trimerous. B3, tetramerous. C-F complex whorled. C, two simple pairs followed by a pair of double positions and a tetramerous whorl. D, two simple pairs followed by two pairs of double positions, a simple pair, and a hexamerous whorl. E, two simple pairs followed by alternating pairs of double positions. F, two simple pairs followed by a pair of triple and a pair of double positions.

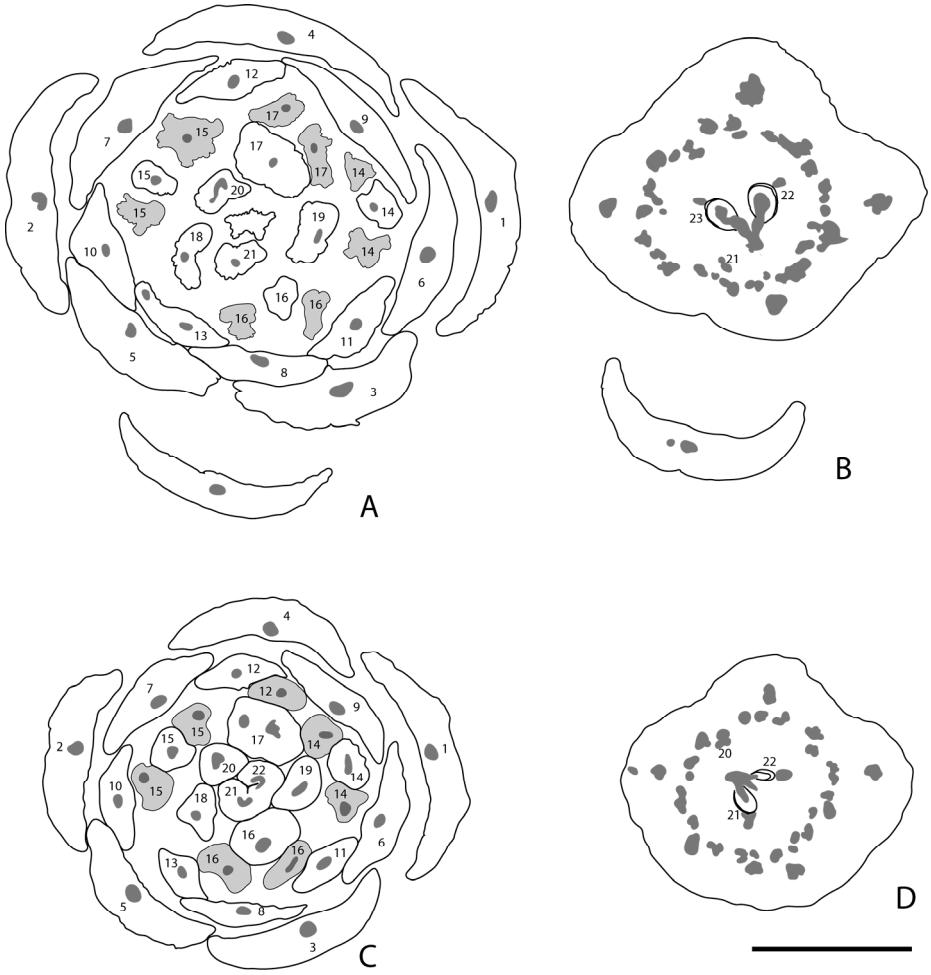

Fig. 4 Gomortegaceae, *Gomortega keule*. Transverse section series of late floral buds. A-B, terminal floral bud. A, level above rim of floral cup. B, level of ovary. C-D, lateral floral bud. C, level above rim of floral cup. D, level of ovary. Dark gray: vasculature; light gray: glandular appendages of stamens (and staminodes); floral organs numbered along ontogenetic spiral. Bar = 1mm.

- *Prophylls*: the first phyllomes (usually bracts) on a lateral branch (commonly two in transverse position in basal angiosperms and eudicots).
- *Staminodes*: stamen-like sterile organs. In Laurales, staminodes are often present between the stamens and the carpels (inner staminodes).
- *Thyrsoid*: determinate thyrse (fig. 2*B*).

To introduce the phyllotaxis terminology we use in the descriptions we first outline basic patterns of floral phyllotaxis that occur in the study group. We distinguish four major kinds of phyllotaxis: (1) spiral, (2) whorled with simple whorls, (3) whorled with complex whorls, and (4) irregular. Patterns (2) and (3) show a diversity of subpatterns.

(1) In the Fibonacci spiral pattern (fig. 3*A*) the organs have an average divergence angle of 137.5° (the angles between two successively formed organs and the floral centre). Often organs of the same kind occur in Fibonacci numbers (2, 3, 5, 8, 13…) and form series in Fibonacci numbers around the circumference of a flower. Series are analogous to whorls in whorled flowers but they are less well circumscribed than whorls, because the distances between the neighboring organs are not all the same (the divergence angle of 137.5° is not a fraction of 360°).

(2) The simple whorled pattern (fig. 3*B1*-3*B3*) has alternating whorls, each with the same number of organs. The divergence angles between the organs within a whorl are constant, always a fraction of 360°. The number of organs (merism) within each whorl can be 2 (dimerous, decussate; fig. 3*B1*), 3 (trimerous; fig. 3*B2*), 4 (tetramerous; fig. 3*B3*), or rarely more. Rarely this number may change within a flower, e.g. from 2 to 3 or from 3 to 2 (by intercalation or loss of an organ from one whorl to the next).

(3) In the pattern with complex whorls (fig. 3*C*-3*G*), double, triple, etc. positions occur, meaning that at the place where a single organ is expected, two (or more) organs are formed in collateral position. (a) A common case starts with two whorls of two organs each, followed by two double positions that alternate with the single organs of the preceding (dimerous) whorl, thus four organs in two

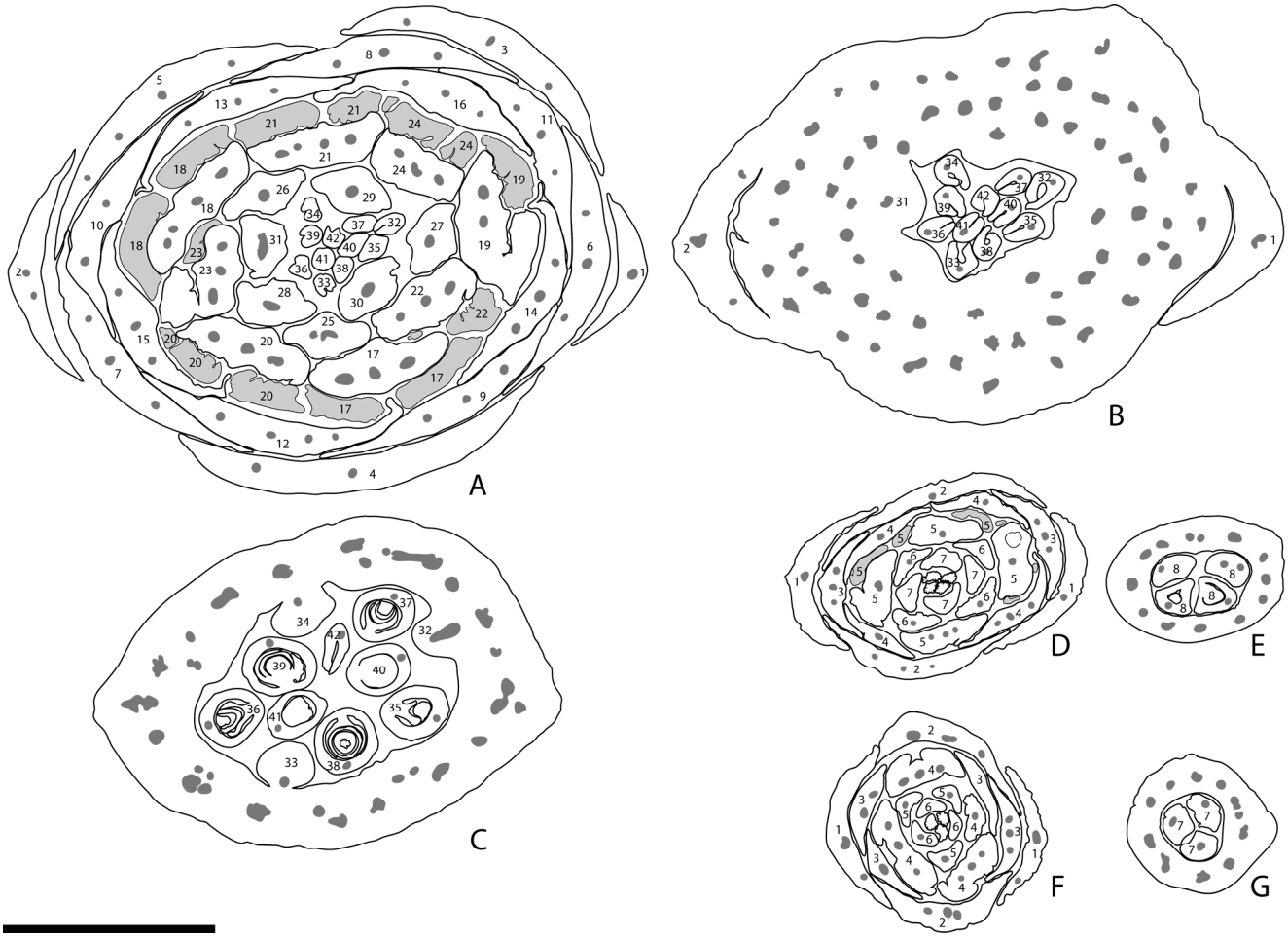

Fig. 5 Atherospermataceae. Transverse section series of late floral bud. A-C, *Daphnandra repandula*, terminal flower. A, level of rim of floral cup. B, level of attachment of innermost staminode. C, level of gynoecium. D, E, *Daphnandra micrantha*, terminal flower. D, level of rim of floral cup. E, level of gynoecium F, G, *Daphnandra micrantha*, lateral flower. F, level of rim of floral cup. G, level of gynoecium. Dark gray: vasculature; light gray: glandular appendages of stamens (and staminodes). A-C, floral organs numbered along ontogenetic spiral. D-G, floral organs numbered according to whorls. Bar = 1mm.

collateral pairs. The subsequent whorl consists again of four organs but all organs now alternate with each of the four organs of the preceding whorl (fig. 3*C*). Thus there is a transition from dimerous to tetramerous whorls via an intermediate whorl with two double positions. Variations of this pattern are: (b) two double positions (four organs) and two simple positions (two organs), followed by six organs alternating with these, thus formation of a hexamerous whorl (fig. 3*D*); (c) double positions can alternate several times in subsequent whorls without changing to simple whorls of double the number of organs (fig. 3*E*); (d) instead of collateral double positions there are collateral triple or even quadruple positions leading to more complex whorled patterns (fig. 3*F*).

(4) In irregular phyllotaxis, no pattern can easily be recognized.

Differentiation between bracts and tepals is usually straightforward in eudicots and monocots, but can be problematic in basal angiosperms (ANITA grade and Magnoliidae). Endress (1980b, c) used four criteria to – arbitrarily - set such delimitations: "(1) beginning of short internodes, (2) change of phyllotaxis from decussate to spiral, (3) beginning of the increase of the size of the phyllomes, (4) beginning of branched vasculature of the phyllomes". We used the following, artificial but practical, working definition: phyllomes are considered to be bracts if they are directly below the floral cup. When several interpretations of the phyllotaxis of a system are possible, we favor the most simple interpretation.

Results

Gomortega (Gomortegaceae)

Gomortega keule - A terminal flower of a botryoid sectioned (fig. 4*A*, 4*B*) is preceded by an empty bract and has 9 tepals, 8 stamens, 4 staminodes and 2 carpels. Floral organs show an average divergence angle of 136.7° (± 20°), in accordance with a Fibonacci spiral pattern (fig. 3*A*; floral diagram fig. 22*A*). Only the two innermost divergence angles are more irregular (206° and 75°). The tepals form two series of five organs (with inclusion of the empty bract immediately preceding the flower), and the stamens form

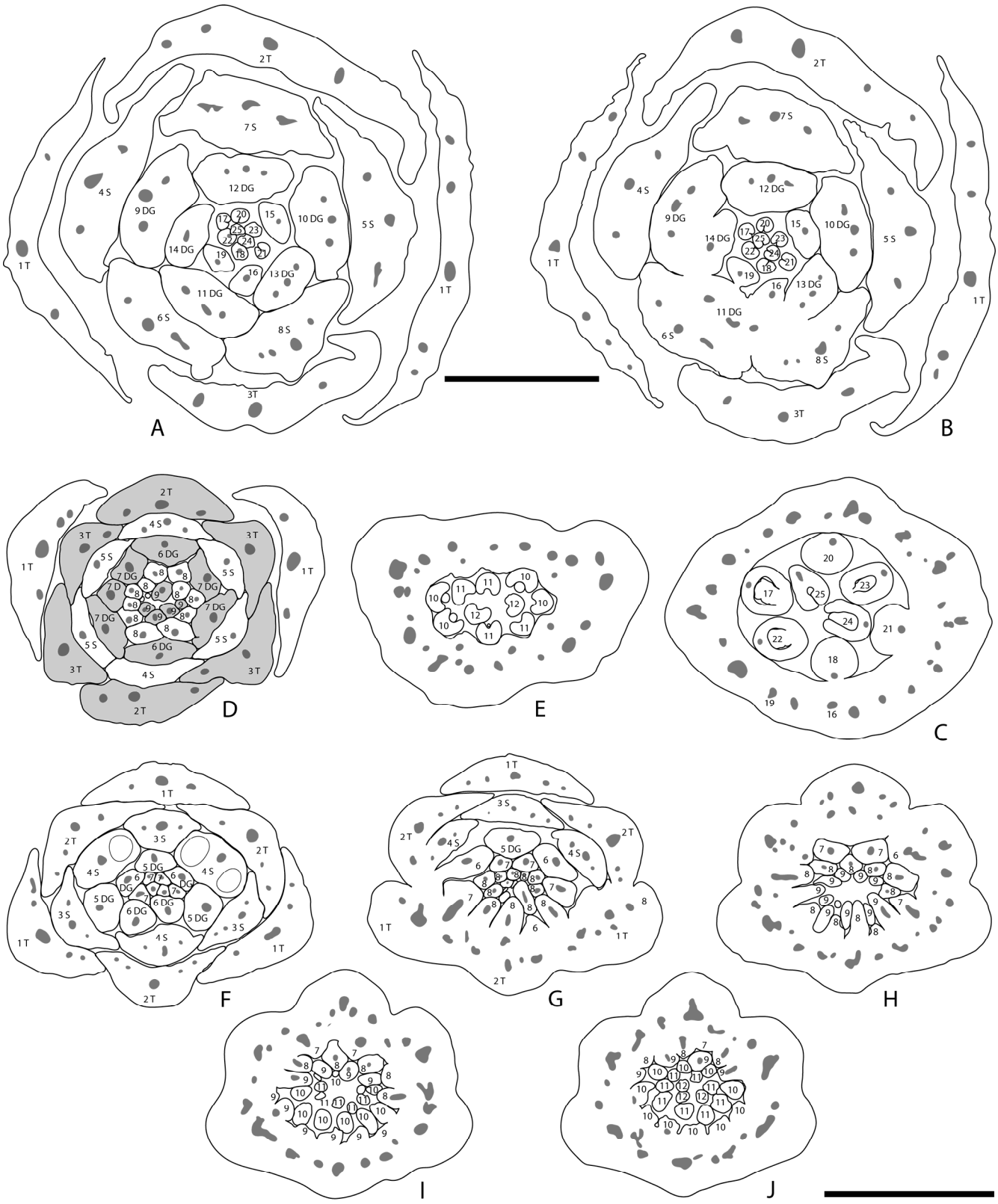

Fig. 6 Atherospermataceae. Transverse section series of floral buds. A-C *Doryphora aromatica*. A, level of rim of floral cup. B, level of base of staminodes. C, level of gynoecium. D, E, *Doryphora sassafras*, terminal flower. D, level of rim of floral cup. E, level of gynoecium. F-J, *Doryphora sassafras*, lateral flower. F, level of rim of floral cup. G-J level of base of staminodes and carpels. Dark gray: vasculature; light gray: selected sets of organ pairs and double positions. T = tepal, S = stamen, DG = staminode with gland. A-C, outer floral organs numbered according to whorls, inner floral organs numbered along ontogenetic spiral. D-G, floral organs numbered according to whorls. Bar = 1mm.

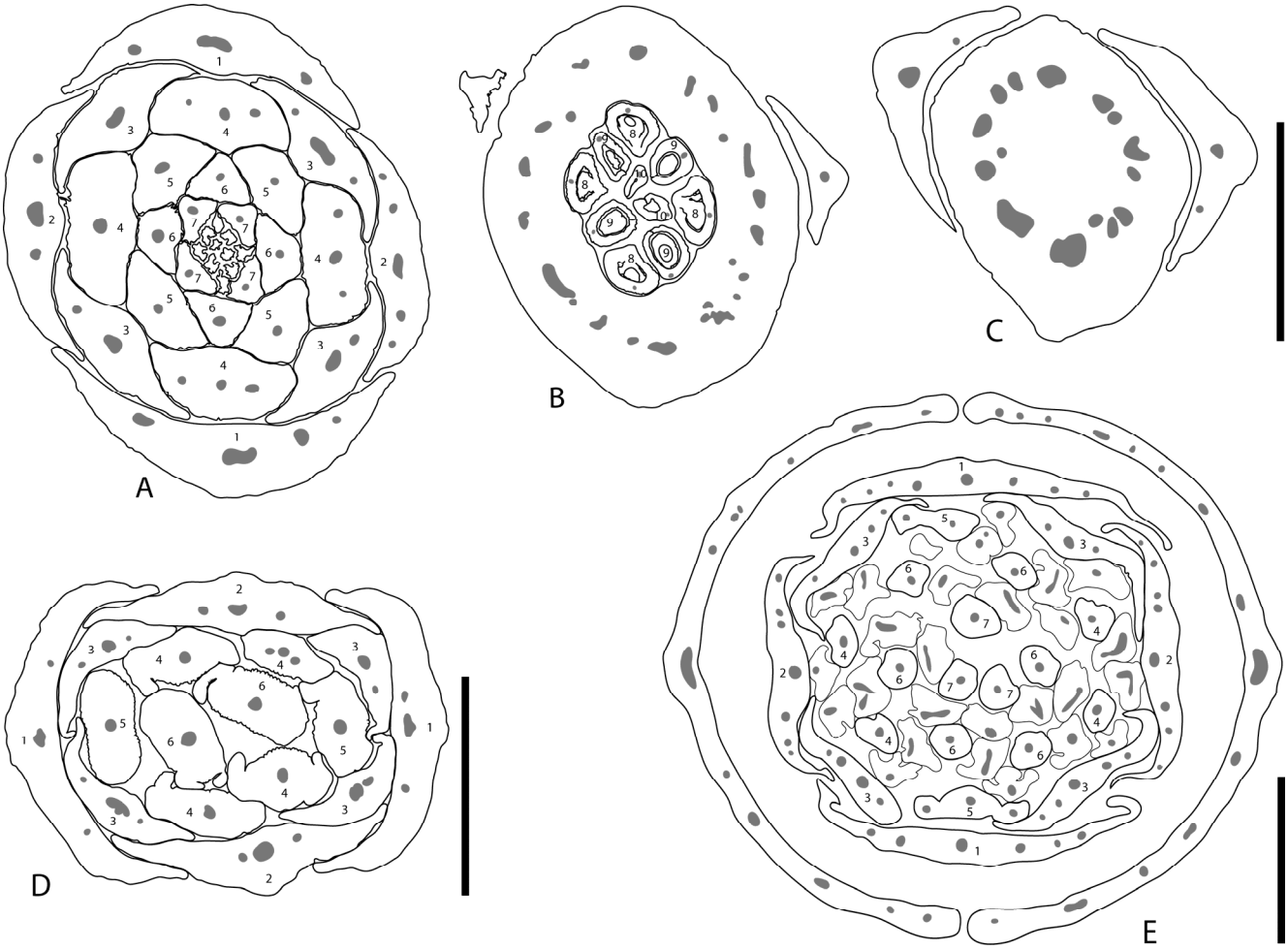

Fig. 7 Atherospermataceae. Transverse section series of late floral bud. A-C, *Dryadodaphne trachyphloia*, lateral floral bud. A, level of rim of floral cup. B, level of gynoecium. C, pedicel. D, *Laurelia sempervirens*, terminal male floral bud, level of rim of floral cup. E, *Atherosperma moschatum*, male floral bud of single-flowered inflorescence, level of rim of floral cup. Gray: vasculature. Floral organs numbered according to whorls. Bar = 1mm.

two series of 5 and 3 organs. Three lateral flowers sectioned (one illustrated in fig. 4*C*, 4*D*) have 7-9 tepals, 8 stamens, 3-4 staminodes, and 2 carpels. As in the terminal flower, the phyllotaxis is Fibonacci spiral; only the two innermost divergence angles are more irregular in all three flowers (mean divergence angles for all organs: 137.0° ± 18°; 138.6°± 25°; 139.6° ± 28°). Organs of the perianth and the androecium tend to be organized in series of 5 and 3 organs.

Daphnandra (Atherospermataceae)

Daphnandra repandula - A probably terminal flower of a thyrsoid sectioned (fig. 5*A*-5*C*) has 16 tepals, 8 stamens, 7 staminodes, and 11 carpels. The two first tepals are opposite. The other floral organs show an average divergence angle of 137.6° (± 8.5°), according to a Fibonacci spiral pattern (fig. 3*A*). Perianth and androecium form series of eight organs. Three flowers of a thyrsoid were cursorily studied: the terminal flower and a primary and a secondary flower of a dichasium of the thyrsoid (flowers 1, 2, and 3 in fig. 2*B*). All flowers have a Fibonacci spiral phyllotaxis. The terminal flower of the thyrsoid has 12 tepals (of which the two first ones are approximately opposite continuing the phyllotaxis of the subtending bracts of the dichasia), 7 stamens, 8 staminodes, and 10 carpels. The primary flower of the dichasium has 11 tepals (of which the two first ones are transverse, approximately opposite), 8 stamens, 6 staminodes, and 11 carpels. The secondary flower of the dichasium has 9 tepals (of which the two first ones are transverse, approximately opposite), 6 stamens, 8 staminodes, and 9 carpels.

Daphnandra micrantha - A probably terminal flower of a thyrsoid sectioned (fig. 5*D*, 5*E*) has 10 tepals, 4 stamens, 8 staminodes, and 4 carpels. Floral phyllotaxis follows fig. 3*C*. The 10 tepals (whorls 1-4) are arranged in a decussate pattern (fig. 5*D*). Whorl 4 has 4 tepals, arranged in 2 double positions (fig. 5*D*). The subsequent organs (4 stamens, 8 staminodes, and 4 carpels) form alternating tetramerous whorls (whorls 5-8). A terminal flower of collection PKE 4327 studied has a fifth, simple pair of tepals. Staminodes are in two whorls (of 3 and 2 organs). Two lateral flowers were studied (one illustrated in fig. 3*F*, 3*G*); the flowers have 6 and 10 tepals, 3 and 4 stamens, 7 staminodes, and 3 and 4 carpels. In both flowers, there is a switch from tetramerous tepal whorls to trimerous staminode whorls (fig. 3*F)*.

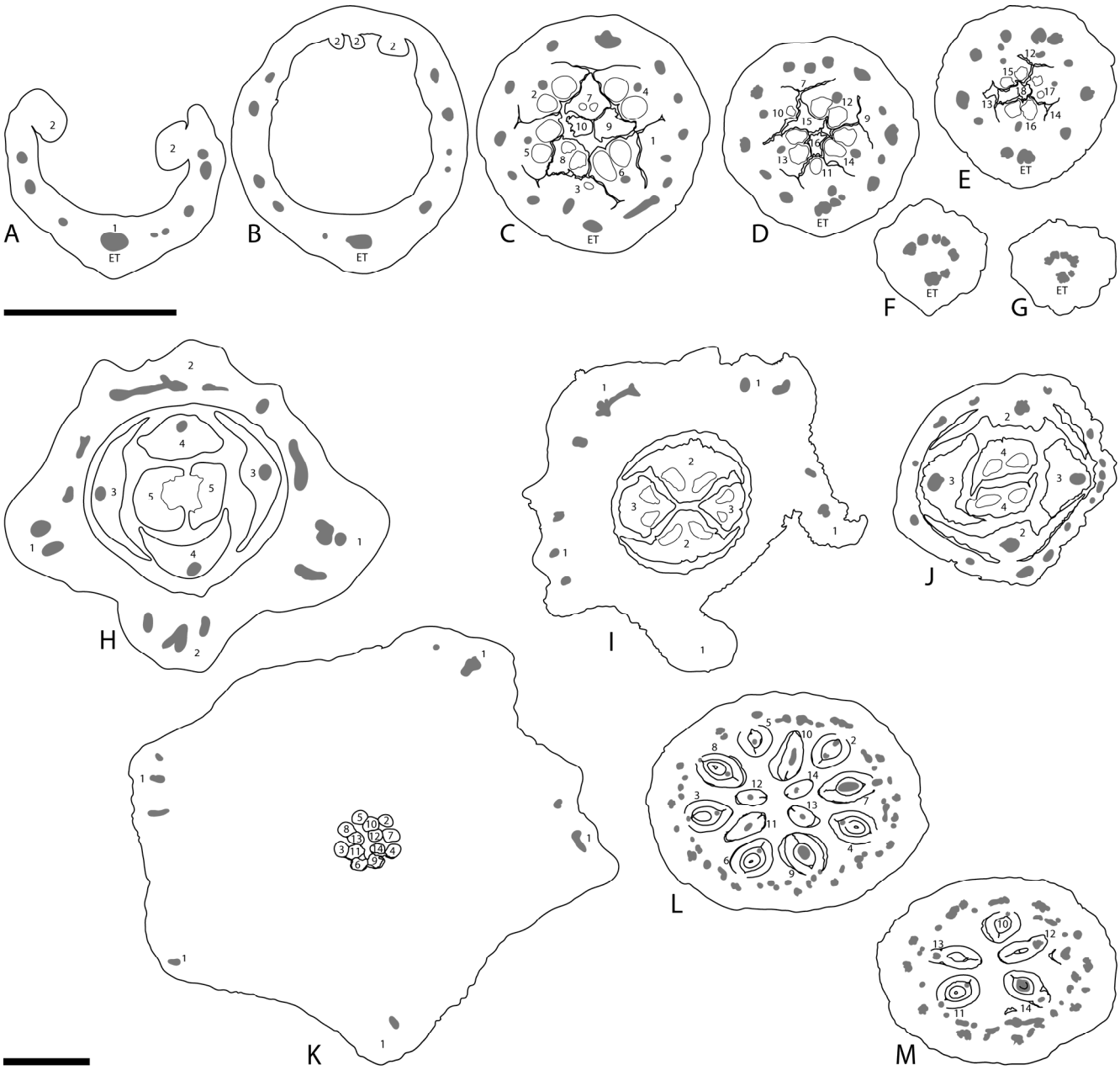

Fig. 8 Siparunaceae. Transverse section series of late floral buds. A-G, *Glossocalyx longicuspis*, male floral bud. A, level base of enlarged tepal and tepals. B, level of rim of floral cup. C-E level of stamens. F, G, level of pedicel. H, *Siparuna thecaphora* first male floral bud, level of rim of floral cup. I, J, *Siparuna thecaphora* second male floral bud. I, level of rim of floral cup. J, level of base of stamens. K-M, *Siparuna thecaophora*, female floral bud. K, level of rim of floral cup. L, M, level of gynoecium. Gray: vasculature. A-G and K-M, outer floral organs numbered according to whorls, inner floral organs numbered along ontogenetic spiral. H-J, floral organs numbered according to whorls. ET = dorsal bundle of enlarged tepal. Bar = 1mm.

Doryphora (Atherospermataceae)

Doryphora aromatica - A flower of a three-flowered botryoid sectioned (fig. 6*A*-6*C*) has 4 tepals, 5 stamens, 9 staminodes (5 with glands and 4 without), and 8 carpels. The tepals form two decussate pairs. Stamens, staminodes, and carpels show an average divergence angle of 139.7° (± 36°), according to a Fibonacci spiral pattern (fig. 3*A*). Unexpectedly, along the ontogenetic spiral, the first two carpels are followed by the last staminode and only then by the remaining carpels (fig. 6*B*). The androecium has two series of five organs (five stamens and five staminodes with glands, see fig. 6*A*). In a sectioned gynoecium of an anthetic flower of collection Hyland 8610 the divergence angle between the innermost three staminodes and seven carpels is 139° (± 18.24°), in accordance with a spiral pattern in the Fibonacci mode. Two cursorily studied flowers of collection Staedler S006-32 have two decussate pairs of tepals, 5 stamens, 10 and 8 staminodes (5 and 4 with glands), and 9 and 12 carpels. The androecium and gynoecium appears to have a Fibonacci spiral phyllotaxis.

Doryphora sassafras - A terminal flower of a 3-flowered botryoid sectioned (fig. 6*D*, 6*E*) has 8 tepals, 6 stamens, 23 staminodes (6 with glands and 17 without), and 10 carpels. The flower appears to have trimerous whorls, but organ

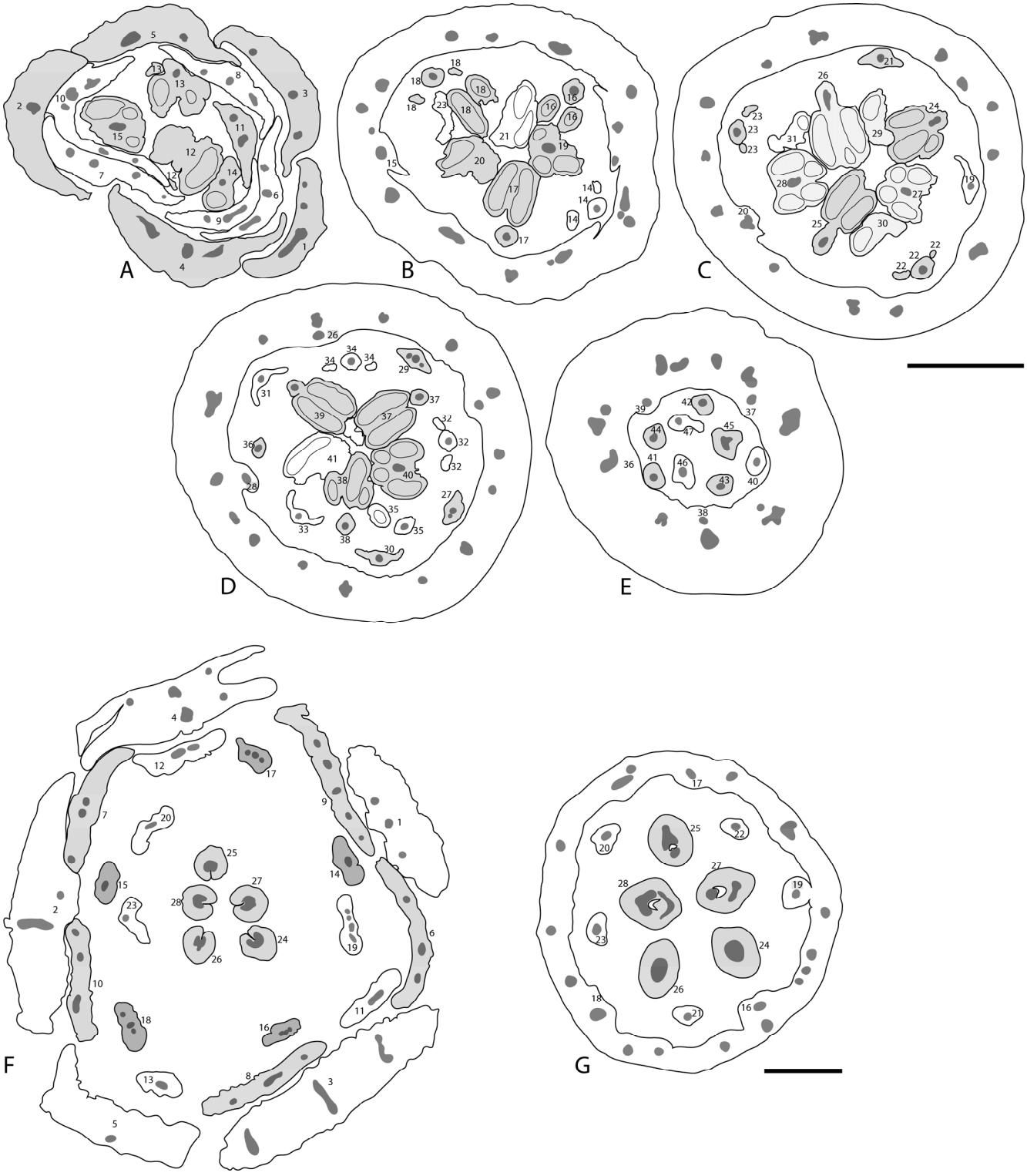

Fig. 9 Monimioideae, Monimiaceae, *Peumus boldus*. Transverse section series of late floral bud and anthetic flower. A-E, male lateral floral bud. A, level of rim of floral cup. B-E, level of androecium. F, G, female terminal anthetic flower. F, level of rim of floral cup. G, level of gynoecium. Dark gray: vasculature; light gray: organs forming a series. Floral organs numbered along ontogenetic spiral. Bar = 1mm.

aestivation suggests a more complex pattern. Floral phyllotaxis follows approximately fig. 3*E* (floral diagram fig. 22*B*). The two outermost tepals are more or less opposite (whorl 1). The subsequent 19 organs (6 tepals, 6 stamens, 7 staminodes [6 with glands, and one without]) form simple decussate pairs and pairs of double positions alternatingly (simple pairs: 2, 4, and 6; pairs of double positions: 3, 5, and 7) (see fig. 6*D*). One of the positions of the last pair with double positions (whorl 7) is in itself doubled and has one staminode with glands and one

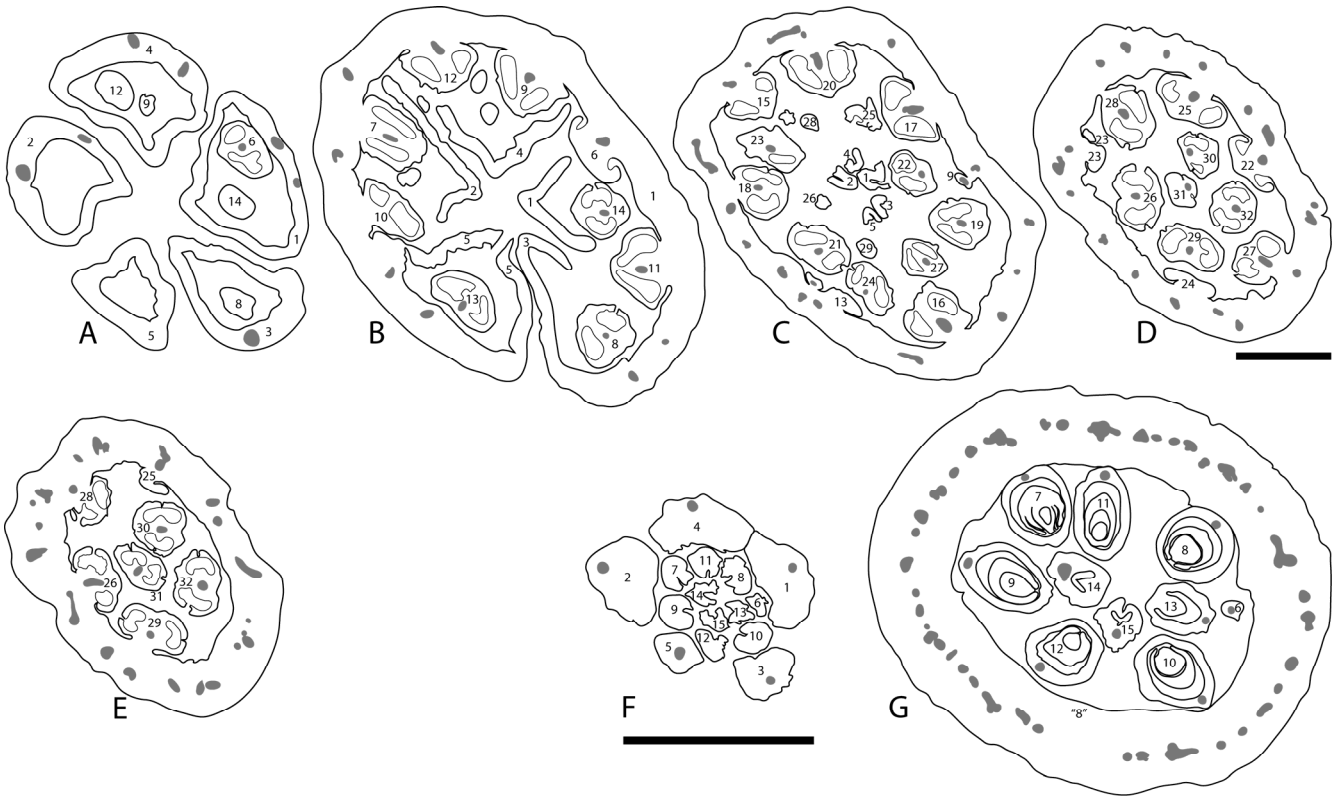

Fig. 10 Monimioideae, Monimiaceae, *Palmeria gracilis*. Transverse section series of late lateral floral buds. A-E, male floral bud. A, B, level of rim of floral cup. C-E, level of androecium. F, G, female floral bud. F, level of rim of floral cup. G, level of gynoecium. Gray: vasculature. Floral organs numbered along ontogenetic spiral. Bar = 1mm.

without glands. The outermost staminodes without glands form an 11-merous whorl (whorl 8). The innermost staminodes (without glands, whorl 9) form a 5-merous whorl. The carpels appear to be arranged in two alternating pairs of double positions (whorls 10 and 11), plus two carpels in the center of the flower (whorl 12, see fig. 6*E*). Three further cursorily studied terminal flowers of three 3-flowered botryoids have 5 or 6 tepals, 6-8 stamens, 17-30 staminodes (5 or 6 with glands, and 12-24 without), and 12-17 carpels. In two of the three flowers, the arrangement of the tepals, stamens, and outermost staminodes is as in the sectioned flower. In addition, a second, simple pair of stamens occurs in one flower and a pair with a stamen and a staminode with glands in the other. In the third flower, stamens and outermost staminodes are in trimerous whorls.

A lateral flower sectioned (fig. 4*F*-4*G*) has 6 tepals, 6 stamens, 31 staminodes (7 with glands and 24 without), and 22 carpels (the identity of the 22 innermost organs is tentative because they are in an early stage of differentiation). Floral phyllotaxis follows approximately fig. 3*D* (floral diagram fig. 22*C*). Trimerous whorls are present in the outer floral organs: tepals (whorls 1 and 2), stamens (whorls 3 and 4), staminodes with glands (whorls 5 and 6), and staminodes without glands (whorl 7). In whorl 1, the unpaired tepal is abaxial. Whorls 6 and 7 have one double position in the median plane each. The staminodes of both whorls 6 and 7 are in contact with the staminodes of whorl 8. Whorls 6 and 7 together form an 8-merous system, which mediates the transition to the higher merism of the inner whorls. The inner organs form three 10-merous whorls (whorl 8-10), one 8-merous whorl (whorl 11), and four carpels in the center (whorl 12). Four cursorily studied young flowers (out of the six lateral flowers of the 3 inflorescences) have 6 tepals, 6 stamens, 6-9 staminodes with glands, and 45-57 still undifferentiated inner organs (staminodes without glands and carpels). The perianth is as in the sectioned flower. Trimerous whorls of staminodes with glands are found in three flowers (with occasional double positions in two flowers); in the fourth flower, hexamerous whorls of staminodes with and without glands are present, and in two other flowers, hexamerous whorls of staminodes without glands.

Dryadodaphne (Atherospermataceae)

Dryadodaphne trachyphloia - A lateral flower of a botryoid sectioned (fig. 7*A*-7*C*) has 8 tepals (preceded by two prophylls), 4 stamens, 12 staminodes, and 10 carpels. Floral phyllotaxis follows fig. 3*C* (floral diagram fig. 22*D*). The prophylls (fig. 7*B*, 7*C*) and the tepals of whorl 1-3 (fig. 7*A*) are decussate. The four tepals of whorl 3 form two double positions (fig. 7*A*). Subsequent organs (4 stamens, 12 staminodes, and the 8 outer carpels) form tetramerous whorls (whorls 4-9), and the two inner carpels a dimerous whorl (whorl 10). In a cursorily studied flower (A. Ford 4791), phyllotaxis and merism is the same as in the sectioned flower. Two other flowers (a terminal and a lateral one; A. Ford 4791) have four inner carpels (instead of two), which form a tetramerous whorl.

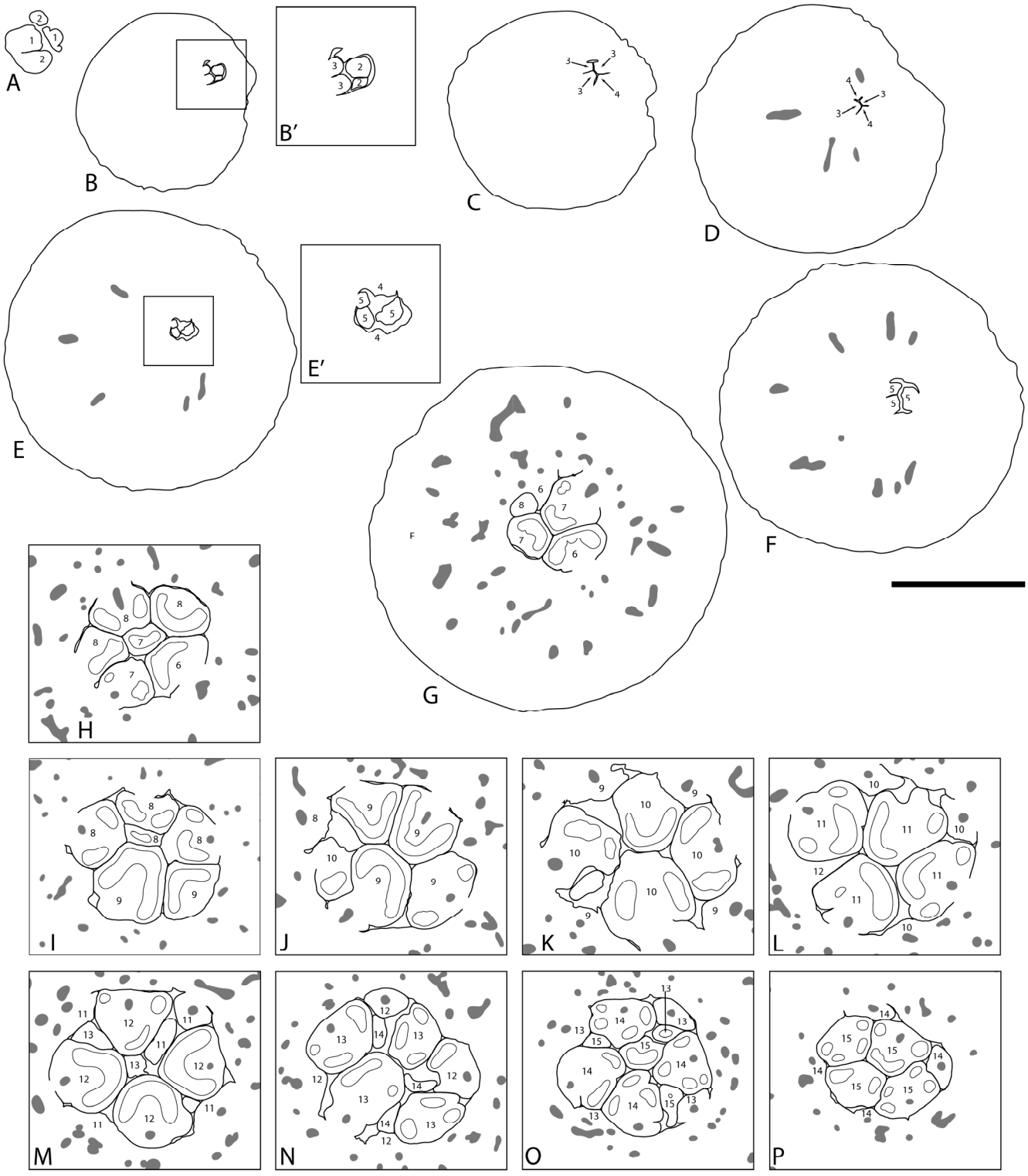

Fig. 11 Mollinedioideae, Monimiaceae, *Tambourissa purpurea*. Transverse section series of late male terminal floral bud. A-F, level of perianth. B', close-up of B. E', close-up of E. G-P, level of androecium. Gray: vasculature. Floral organs numbered according to whorls. B', E', bar = 0,5mm. A, B, C, D, E, F-P, bar = 1mm.

Laurelia (Atherospermataceae)

Laurelia sempervirens - A terminal flower of a male botryoid sectioned (fig. 7*D*) has 8 tepals and 8 stamens. Floral phyllotaxis follows approximately fig. 3*C*. Floral phyllotaxis is decussate (whorls 1-5), except for the two innermost stamens (whorl 6). The two outer tepal whorls are simple pairs (whorls 1 and 2), the inner four tepals and the outer four stamens are in double positions (whorls 3 and

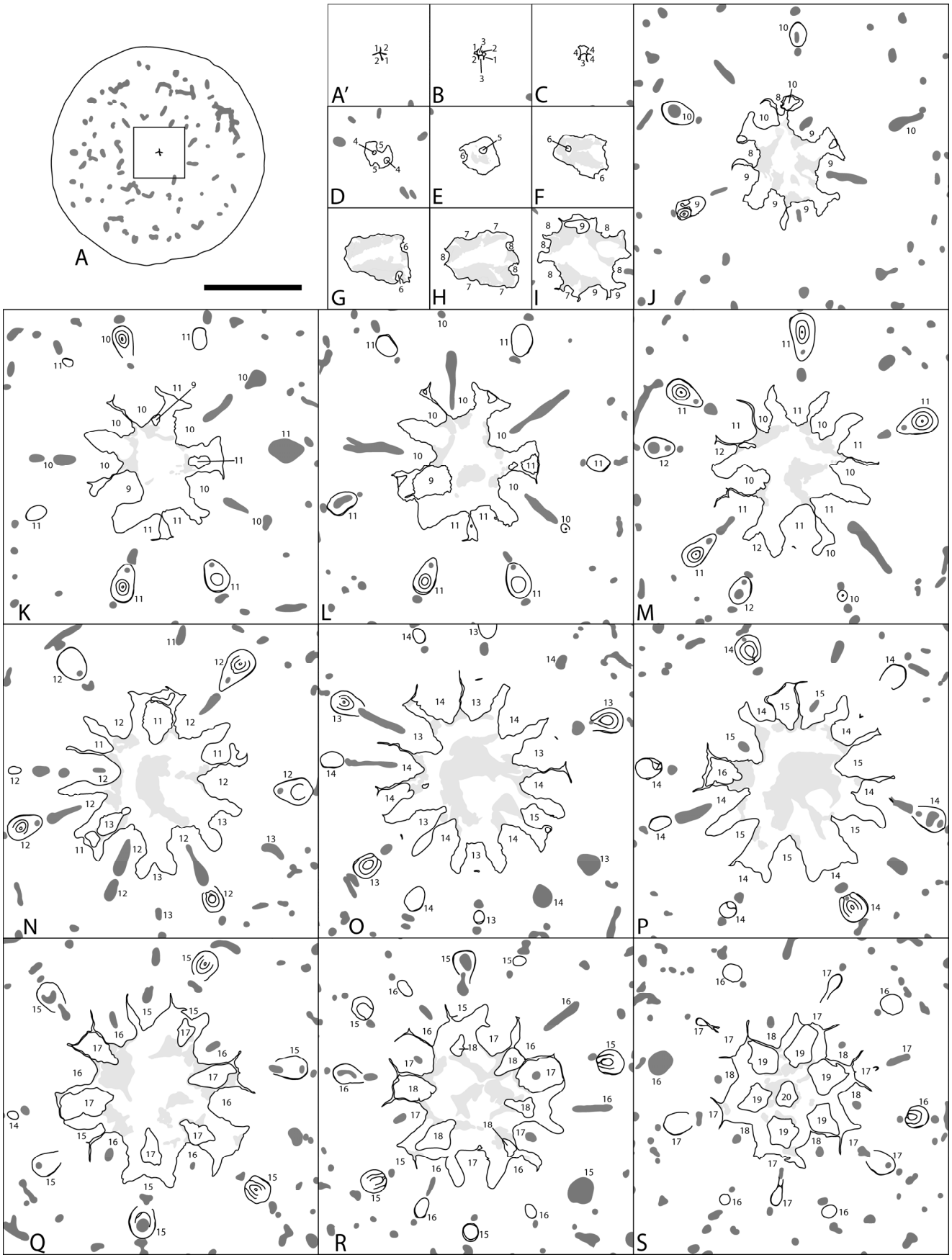

Fig. 12 Mollinedioideae, Monimiaceae, *Tambourissa purpurea*. Transverse section series of late female floral bud. A-G, level of perianth. H, I, level of carpellodes. J, level of carpels and carpellodes. K-S, level of carpels. A', close-up of A. Dark gray: vasculature; light gray: secretion. Floral organs numbered according to whorls. A, bar = 2mm. A'-S, bar = 1mm.

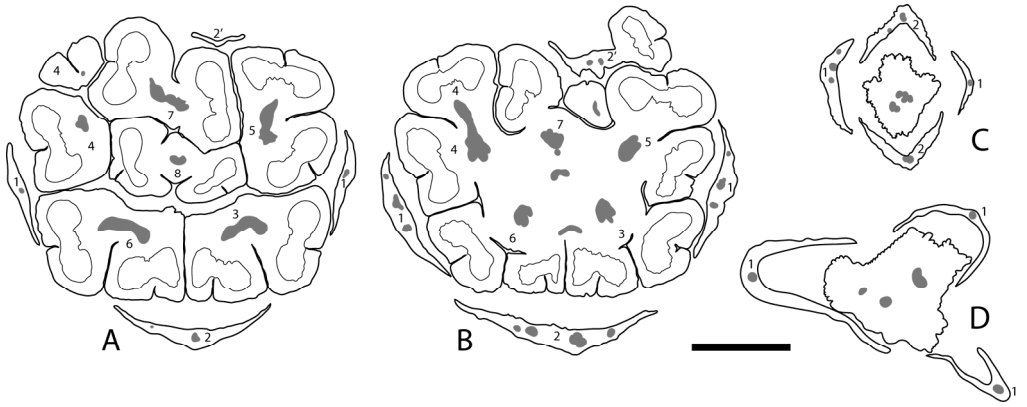

Fig. 13 Mollinedioideae, Monimiaceae, *Xymalos monospora*. Transverse section series of late floral buds. A, B, terminal male floral bud, level of androecium. C, first female floral bud, level of rim of floral cup. D, second female flower, level of rim of floral cup. Gray: vasculature. A, B, outer floral organs numbered according to whorls, inner floral organs numbered along ontogenetic spiral. C, D, floral organs numbered according to whorls. Bar = 1mm.

4). The stamens of whorl 5 are a simple pair. Four cursorily studied flowers have 6 and 8 tepals, and 6, 10, or 11 stamens. Two flowers have a decussate phyllotaxis with double positions in the center; tetramerous whorls of stamens are only present in the flowers with the highest number of organs (the terminal flower and one large lateral flower). The four outer tepals are always decussate. In lateral flowers with more organs (lower lateral flowers), the four inner tepals are in two double positions. The four outer stamens are in two double positions in all flowers studied. The inner stamens form a pair (upper lateral flower), or two decussate pairs (lower lateral flower), or a pair followed by a tetramerous whorl (lower lateral flower), or a tetramerous whorl followed by three stamens (terminal flower).

Atherosperma (Atherospermataceae)

Atherosperma moschatum - A male flower of a one-flowered inflorescence sectioned (fig. 7*E*) has 8 tepals (preceded by two prophylls), and 15 stamens. Floral phyllotaxis follows approximately fig. 3*D*. The organs of whorls 1-5 are decussate. However, the four tepals of whorl 3 and the four stamens of whorl 4 are in double positions. The six stamens following whorl 5 form a hexamerous whorl (whorl 6), alternating with the six organs of whorls 4 plus 5. The three inner stamens form whorl 7. In three cursorily studied flowers of three single-flowered inflorescences, each flower is preceded by two prophylls. In all three flowers, the eight tepals are decussate (whorls 1-3), whorl 3 with double positions. The number of stamens and their arrangement is variable. In one flower the 12 stamens form three tetramerous whorls. In another flower, the 14 stamens form two alternating double positions, a tetramerous whorl and a dimerous whorl. In the third flower, the 18 stamens form three decussate whorls (whorls 5 and 6 with double positions), and two tetramerous whorls.

Glossocalyx (Siparunaceae)

Glossocalyx longicuspis - A male flower sectioned (fig. 8*A*-8*G*) has one enlarged tepal, 5 small tepals, and 18 stamens. The tepals appear to be arranged in a whorl. The stamens show an average divergence angle of 138.4° (± 11°), according to a Fibonacci spiral pattern (fig. 3*A*; floral diagram fig. 22*E*). The tepals have the shape of short knobs. They and the tip of the enlarged tepal are covered with hairs that are denser and shorter than on the rest of the floral surface. The small tepals and the tip of the enlarged tepal stain intensely violet with ruthenium red and toluidine blue, suggesting a secretory function. The vascular trace of the enlarged tepal can be followed from its insertion on the rim of the floral cup down to the base of the peduncle, much further down than the vascular trace of the other tepals extend before they form a stele. No floral subtending bract is found on the peduncle or at its base. A second flower from the same collection sectioned has one enlarged tepal, 4 small tepals, and 17 stamens. Tepal indument and histology are as in the first flower. The stamens appear to form a Fibonacci spiral pattern. Three cursorily studied flowers from the same collection have the same structure, except for one with five small tepals. It is not possible to determine the position of the studied flowers in the ramification system because of cauliflory.

Siparuna (Siparunaceae)

Siparuna thecaphora - Two male flowers sectioned (flower 1 fig. 8*H*, and flower 2 fig. 8*I*, 8*J*; Floral diagrams fig. 22*F*, 22*G*) have 4 and 5 tepals, and 6 stamens. In flower 1, the tepals are decussate (whorl 1 and 2). In flower 2, they are in a pentamerous whorl (whorl 1, fig. 8*I*); their insertion at different levels on the floral base suggests spiral initiation. In both flowers, the stamens form three decussate pairs (whorls 3-5 in flower 1). Ten additional flowers of two inflorescences (five flowers of each; collection PKE 1202) have 4 or 5 tepals and 5 or 6 stamens. The terminal flower of a thyrsoid (with two lateral monochasia) has 5 tepals. For flowers of various positions in the monochasia, tepal number is not related to flower position. In the flowers of one inflorescence, the 5-6 stamens are decussate, but in those of the other they form a tetramerous whorl alternating with the tepals of whorls 1 plus 2, and one or two stamens in the center.

A female flower sectioned (fig. 8*K*-*M*) has 5 tepals, and 13 carpels. Tepals form a pentamerous whorl (whorl 1).

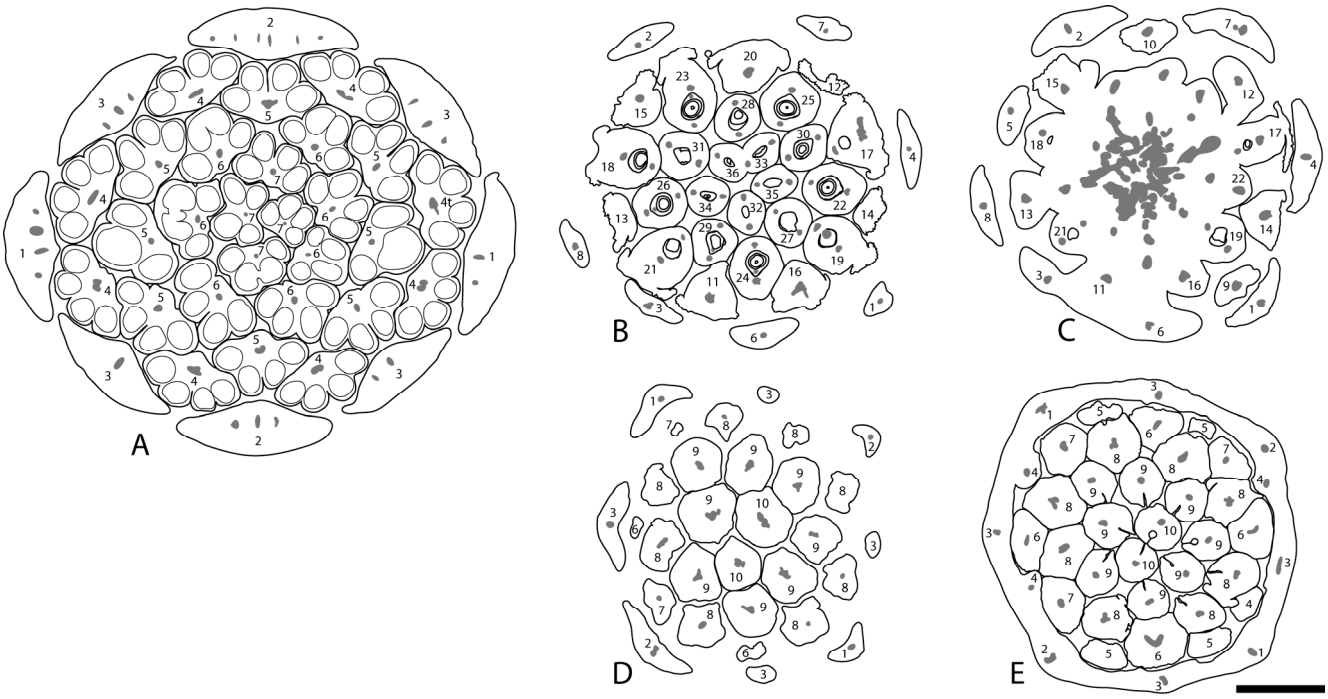

Fig. 14 Mollinedioideae, Monimiaceae, *Hedycarya angustifolia*. Transverse section series of late floral buds, and anthetic flower. A, lateral male floral bud, level of base of inner stamens. B, C, first female flower of single flowered inflorescence. B, level of base of inner carpels, C, level of base of tepals. D, E, second female flower of single flowered inflorescence. D, level of base of tepals. E, level of base of outer carpels. Gray: vasculature. A, D, E, floral organs numbered according to whorls. B, C, floral organs numbered along ontogenetic spiral. Bar = 1mm.

They are inserted at different levels on the floral cup, which suggests spiral initiation. The first 9 carpels show an average divergence angle of 138.7° (± 9°), according to a Fibonacci spiral pattern (fig. 3*A*). The inner four carpels have more irregular positions. Carpels form series of eight and five organs. Two other sectioned flowers (collection PKE 1301) have 4 and 6 tepals, and 11 carpels; the nine outermost carpels have a Fibonacci spiral phyllotaxis (average divergence angle 135.1° ± 13° and 137.9°± 17°). Nine cursorily studied lateral flowers from three inflorescences (collection PKE 1203) have 5 tepals (eight flowers) or 6 tepals (one flower), and 9 (two flowers), 10 (six flowers) or 11 carpels (one flower). Organ number does not appear to depend on the position in the ramification system. Series of five carpels are common.

Peumus (Monimioideae, Monimiaceae)

Peumus boldus – A lateral flower of a male botryoid sectioned (fig. 9*A*-9*E*) has 11 tepals, and 36 stamens, with an average divergence angle of 137.1° (± 11°), according to a Fibonacci spiral pattern (fig. 3*A*). The floral organs form series of five organs: two series of tepals, one series including the last tepal and four stamens (fig. 9*A*), and seven series of stamens (fig. 9*B*-9*E*). Five cursorily studied flowers have 10-16 tepals and 34-43 stamens. The terminal and the lateral flower of an intact part of a botryoid do not differ from each other. Tepals form series of 3, 5, and 8 organs (commonly five).

A terminal flower of a female botryoid sectioned (fig. 9*F*, 9*G*) has 12 tepals, 11 staminodes, and 5 carpels, with an average divergence angle of 137.7° (± 12°), according to a Fibonacci spiral pattern (fig. 3*A*). Tepals, staminodes, and carpels form four series of five organs (fig. 9*F*, 9*G*). Only the two inner tepals and the outermost staminode are arranged in a series of three organs (fig. 9*F*). Seven cursorily studied flowers have 10-13 tepals, 10-13 staminodes, and 4-6 carpels. The terminal flower of a partial botryoid has more organs than two lateral flowers (13 versus 10 and 11 tepals, and 6 versus 4 and 5 carpels). Staminode number does not differ between terminal and lateral flowers. Tepals form series of five and eight organs, and staminodes mostly series of five organs.

Palmeria (Monimioideae, Monimiaceae)

Palmeria gracilis - A probably lateral flower of a male botryoid sectioned (fig. 10*A*-10*E*) has 5 tepals, and 27 stamens, with an average divergence angle of 136.8° (± 19°), according to a Fibonacci spiral pattern (fig. 3*A*). The tepals form a series. Three cursorily studied flowers have 4, 5, or 6 tepals, and 21 or 23 stamens. The terminal flower has the smallest organ number. Floral phyllotaxis is Fibonacci spiral in all flowers. Stamens are arranged in series of eight (outer stamens) and five (inner stamens).

A probably lateral flower of a female botryoid sectioned (fig. 10*F*-10*G*) has 5 tepals, 1 carpellode, and 9 carpels. Floral organs show an average divergence angle of 135.9° (± 13°), according to a Fibonacci spiral pattern (fig. 3*A*). There is a missing position in the ontogenetic spiral (position eight, third carpel). Three cursorily studied flowers have 5 tepals, and 8, 9 or 10 carpels. The terminal flower of the three has the smallest number of carpels. Floral phyllotaxis is also Fibonacci spiral.

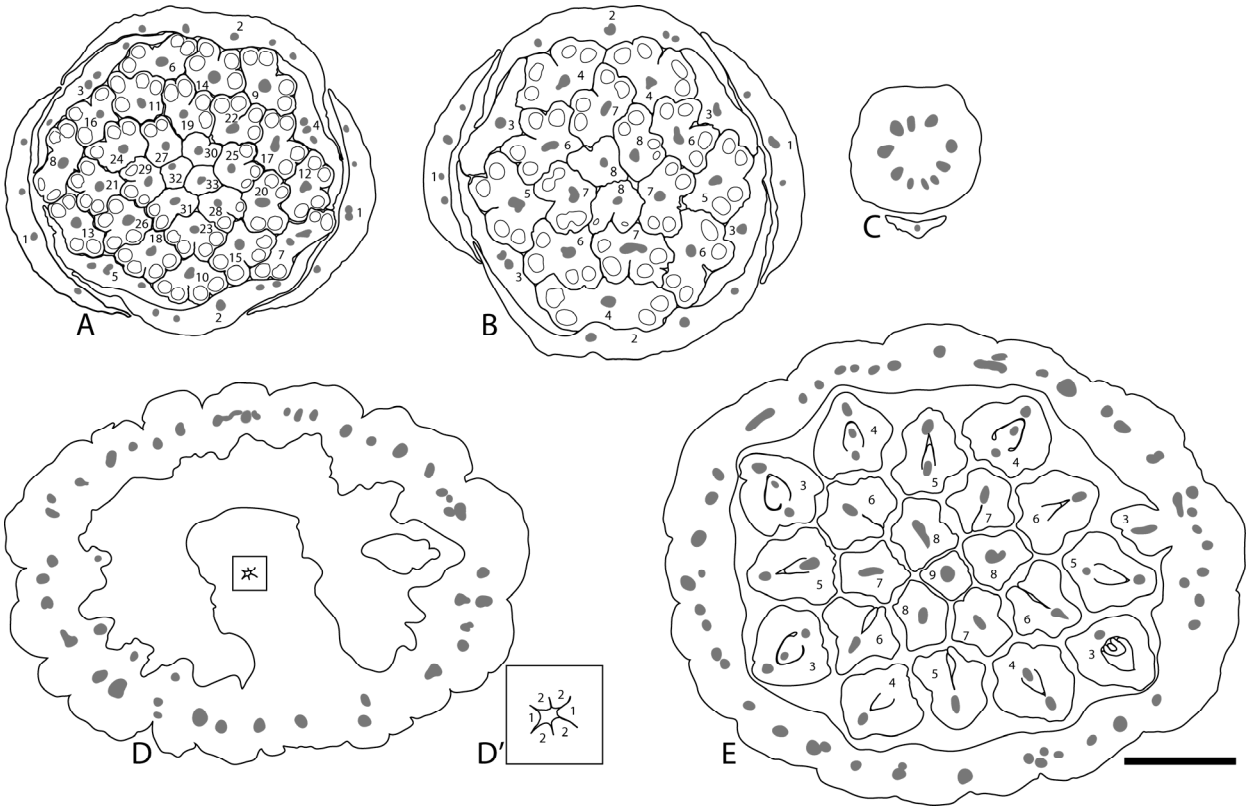

Fig. 15 Mollinedioideae, Monimiaceae, *Levieria acuminata*. Transverse section series of late floral buds. A, terminal male floral bud, level of base of inner stamens. B, C, lateral male floral bud. B, level of base of inner stamens. C, pedicel. D-E, terminal female floral bud. D, D', level of tepals. E, level of gynoecium. Gray: vasculature. A, outer floral organs numbered according to whorls, inner floral organs numbered along ontogenetic spiral. B-E, floral organs numbered according to whorls. A, B, C, D, E, bar = 1mm. D', bar = 0,33mm.

Tambourissa (Mollinedioideae, Monimiaceae)

Tambourissa purpurea - A terminal flower of a three-flowered male botryoid sectioned (fig. 11*A*-11*P*) has 13 tepals and 34 stamens. Floral phyllotaxis follows approximately fig. 3*C*. The tepals in whorls 1-6 are decussate, and whorls 3 and 5 have one of the two positions doubled. Phyllotaxis of the last tepals and first stamens is difficult to interpret, although it appears to follow a decussate pattern. The last tepal and the first stamen form whorl 6. Two stamens form whorl 7. Three stamens form a pair with a double position on one side (whorl 8). The four stamens of whorl 9 alternate with the stamens of whorl 8, having another double position. The next 24 stamens (whorls 10-15) form tetramerous whorls. Eight flowers cursorily studied (collection S08-01) have 23 to 26 stamens (five lateral flowers) or 31 and 32 stamens (three terminal flowers). Most stamens appear to be arranged in tetramerous whorls.

A female flower sectioned (fig. 12*A*-12*S*) has 29 outer sterile organs (the outer 18 of which are tepals, the inner 11 are secretory and vascularized and are here named carpellodes although they do no possess a locule, see discussion), 1 carpellode with a locule, and 61 carpels. Floral phyllotaxis follows approximately fig. 3*E*. The outermost four tepals are decussate (whorls 1 and 2). The two tepals of whorl 3 are not on the same radii as the tepals of whorls 1 and 2, but in between. The next 15 organs (whorls 4-8) are decussate. One of the positions is doubled in whorls 4, 6, and 7. Phyllotaxis of the carpellodes and first carpels is difficult to interpret, although it appears to follow a decussate pattern.Whorl 8 has five carpellodes in a double and a triple position. Whorl 9 has five organs (four carpellodes and a carpel), two carpellodes and the carpel in a triple position, two carpellodes in a double position. Whorl 10 also has five organs (two carpellodes without locule, the carpellode with locule, and two carpels), three of which in a triple position (two carpels and a carpellode), the other two alternate with two organs of whorl 9.The six carpels of whorl 11 alternate with the organs of whorl 10 and form one double position. The next 51 carpels form nine 6-merous whorls (whorls 12-19), three of which (whorls 12, 14 and 15) with one double position. The double positions of whorl 12 and 14 are on the same orthostichy. One carpel is in the center of the flower (whorl 20). Three flowers cursorily studied (collection S08-01) have 61, 67, 71 carpels. Twelve to 13 orthostichies are present which suggests arrangement in alternating hexamerous whorls. In two flowers, the number of orthostichies first increases and then decreases towards the center of the flower.

Tambourissa comorensis - A fragment of a female flower sectioned shows alternating sets of parastichies of similar steepness, although there are irregularities. This suggests a whorled or irregular phyllotaxis.

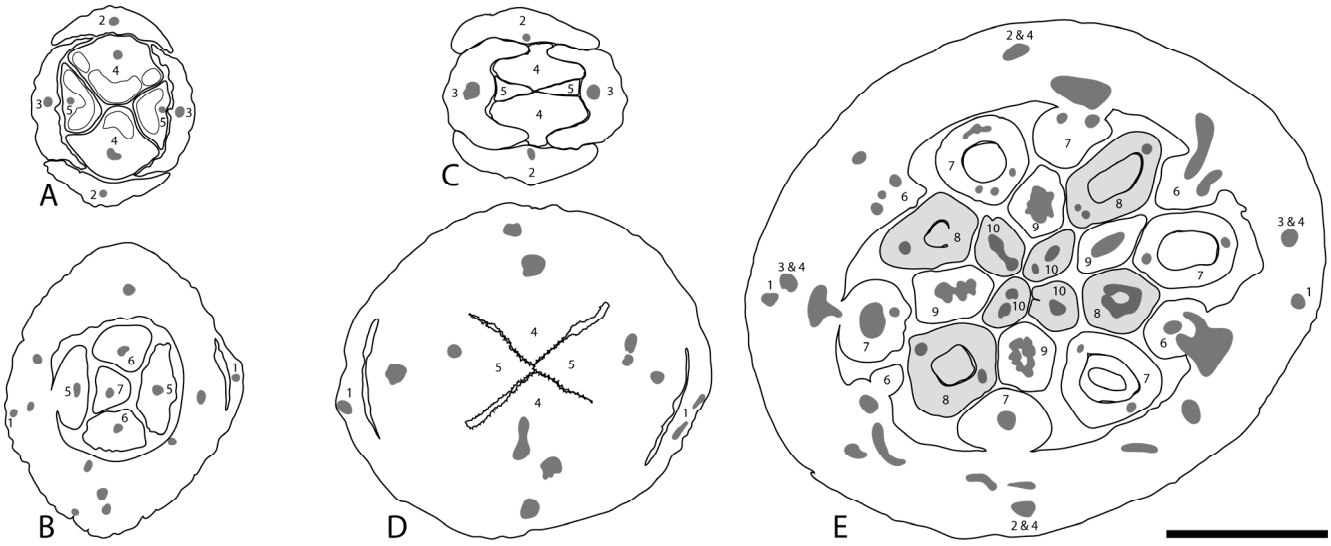

Fig. 16 Mollinedioideae, Monimiaceae. Transverse section series of late floral buds. A, B, *Kibara coriacea*, lateral male floral bud. A, level of rim of floral cup. B, level of androecium. C-E, *Kibara macrophylla*, lateral floral bud. C, D, level of base of tepals. E, level of gynoecium. Dark gray: vasculature; light gray: selected whorls of carpels. Floral organs numbered according to whorls. Bar = 1mm.

Tambourissa ficus - A fragment of a female flower sectioned shows no parastichies, which suggests irregular phyllotaxis.

Xymalos (Mollinedioideae, Monimiaceae)

Xymalos monospora - A terminal flower of a male thyrsoid with accessory flowers sectioned (fig. 13*A*, 13*B*) has 3 tepals and 7 stamens (the first stamen with only one theca). The outermost four organs form whorl 1 and 2. The seven stamens show an average divergence angle of 138.9° (± 17°), according to a Fibonacci spiral pattern (fig. 3*A*). The 17 cursorily studied flowers of the distal portion of a male inflorescence (flowers of all three ramification orders and accessory flowers of the seond order) have 1 to 5 (or 0 to 4, see below) tepals and 3 to 15 stamens. In lateral flowers there is always a tepal-like organ in median abaxial position, which may represent the subtending bract of the flower. Some flowers may be atepalous if this interpretation is correct. The highest organ number is found in the primary flowers of the dichasia, the smallest organ number is found in accessory flowers. The terminal flower has four tepals and 8 stamens. Most flowers have spiral phyllotaxis, even when organ number is very low; but an irregularly whorled pattern (tetramerous) is present in the outer stamens of flowers with an even number of tepals.

Two lateral flowers of a female botryoid sectioned (flower 1, fig. 13*C*, and flower 2, fig. 13*D*) have 3 and 4 tepals, and 1 carpel. In flower 1, the tepals form a trimerous whorl (whorl 1). In flower 2, the tepals are decussate (whorl 1 and 2). Ten cursorily studied flowers have 2-6 tepals (mostly 4) and 1 carpel. Tepals are decussate. Three terminal flowers have four tepals and two preceding empty bracts.

Hedycarya (Mollinedioideae, Monimiaceae)

Hedycarya angustifolia - A probably lateral flower of a male botryoid sectioned (fig. 14*A*; floral diagram fig. 22*H*) has 8 tepals and 27 stamens. Floral phyllotaxis follows approximately fig. 3*C*. The tepals form two simple pairs (whorls 1 and 2) and a pair of two double positions (whorl 3). The outer eight stamens form a whorl of four double positions (whorl 4). The next eight stamens alternate with the outer ones and thus form an octomerous whorl (whorl 5), followed by a heptamerous whorl (whorl 6), in which most stamens alternate with those of whorl 5. Four stamens are in the center of the flower (whorl 7). A terminal and two lateral cursorily studied flowers have 8 tepals, and 29-32 stamens. In all flowers the outer stamens form a whorl of four double positions (in one flower, one double position is replaced by a single position). The whorl of double positions is followed by a whorl of 7, 8 or 9 organs: organ number then decreases toward the center of the flower to 7-, 6-, or 4-merous whorls. Terminal and lateral flowers do not obviously differ in organ number.

A female flower of a one-flowered inflorescence sectioned (fig. 14*B*, 14*C*) has 9 tepals, 9 carpellodes, and 18 carpels, with an average divergence angle of 138.5° (± 18°), according to a Fibonacci spiral pattern (fig. 3*A*). Along the ontogenetic spiral, the two first carpels are followed by the last carpellode and only then by the remaining carpels. Another female flower of a single-flowered inflorescence sectioned (fig. 14*D*, 14*E*) has 8 tepals, 11 carpellodes, and 18 carpels. Floral phyllotaxis follows fig. 3*E*. The tepals form two simple pairs (whorls 1 and 2) and a pair of double positions (whorl 3). The outer eight carpellodes form two alternating pairs of double positions (whorls 4 and 5). The next seven carpellodes form two tetramerous whorls (whorls 6 and 7); there is a carpellode missing in whorl 6. The 16 outer carpels are arranged in two octomerous whorls (whorls 8 and 9). Two carpels are in the center of the flower (whorl 10). Five cursorily studied flowers have 6 (one flower) or 8 tepals (four flowers), and 18-51 carpellodes and carpels. In the two flowers with the highest organ number (45 and 51 carpels and carpellodes), Fibonacci

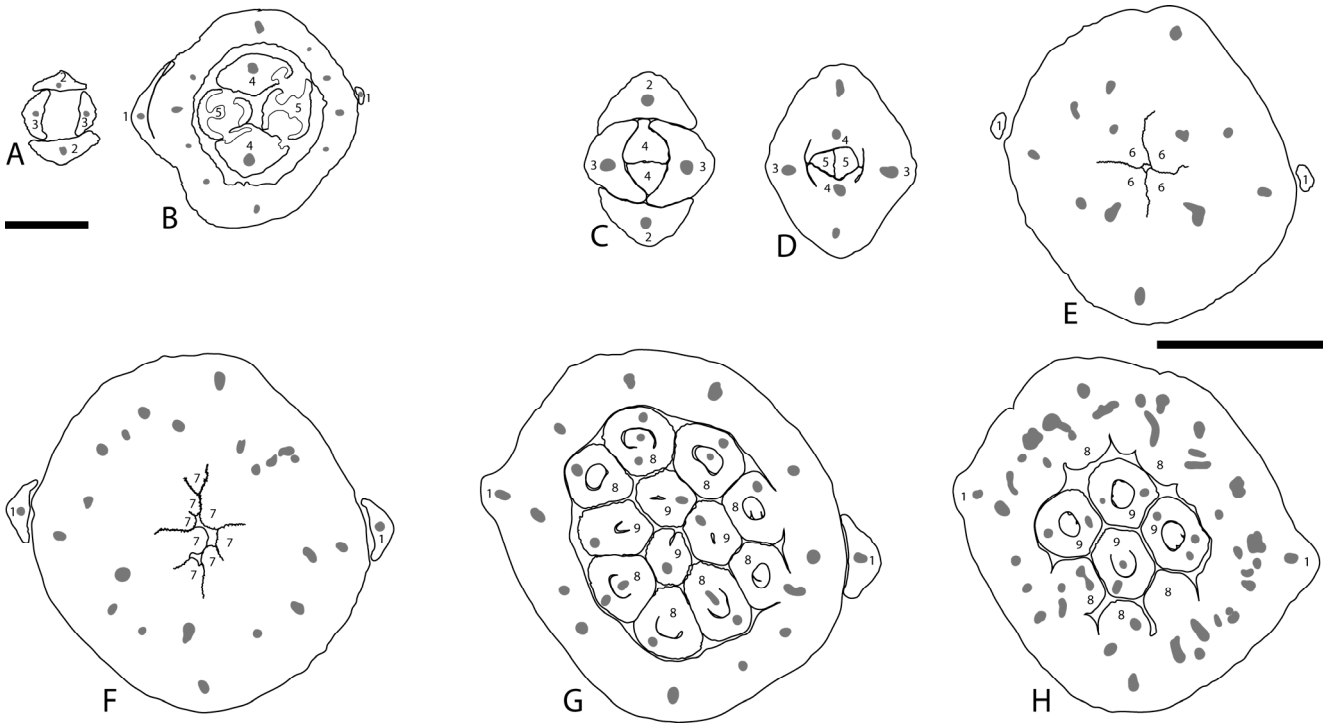

Fig. 17 Mollinedioideae, Monimiaceae, *Wilkiea angustifolia*. Transverse section series of anthetic flowers. A, B, male flower. A, level of rim of floral cup. B, level of androecium. C-H, female flower. C-F, level of tepals. G, H, level of gynoecium. Gray: vasculature. Floral organs numbered according to whorls. Bar = 1mm.

spiral phyllotaxis appears to be present, in contrast to 4- to 9-merous whorls in the other three flowers. In flowers with whorled phyllotaxis, the number of carpellodes and carpels per whorl increases (to 7-9) and then decreases (to 5 or 4) towards the center of the flower.

Levieria (Mollinedioideae, Monimiaceae)

Levieria acuminata - A terminal flower of a male botryoid sectioned (fig. 15*A*) has 7 tepals and 28 stamens. The outer four tepals are decussate (whorl 1 and 2). The three inner tepals and the stamens show an average divergence angle of 136.9° (± 20°), according to a Fibonacci spiral pattern (fig. 3*A*; floral diagram fig. 22*I*). A lateral flower sectioned (fig. 15*B*, 15*C*) has 8 tepals, and 16 stamens. Floral phyllotaxis follows fig. 3*E* (floral diagram fig. 22*J*). The tepals (whorls 1-3) and the outer five stamens (whorls 4 and 5) are decussate. The two tepals of whorl 1 are in lateral position as expected in the absence of prophylls. The positions of whorl 3 and one position of whorl 4 are doubled. The eleven inner stamens form two tetramerous whorls (whorls 6 and 7), and a group of three stamens in the center of the flower (whorl 8). Five cursorily studied flowers have 5-8 tepals, and 14-32 stamens. In the four lateral flowers studied, the two outermost tepals are in lateral position as would be expected in the absence of prophylls. Spiral phyllotaxis is present in the two flowers with the highest number of stamens (a terminal and a large lateral flower with 30 and 32 stamens). In both flowers, the outer four tepals are decussate, and the inner three tepals and the stamens are spiral. Whorled phyllotaxis occurs in the flowers with the smallest number of stamens (14, 16, and 18). The tepals and outer stamens are decussate. The inner three or four tepals, and the outer four stamens are in double positions. The subsequent stamens form a 6- or 8-merous whorl, and the inner stamens a 3-, 4-, or 6-merous whorl.

A terminal flower of a female botryoid sectioned (fig. 15*D*-15*E*) has 6 tepals, and 23 carpels. Floral phyllotaxis follows approximately fig. 3*E* (floral diagram fig. 22*K*). The six tepals (whorls 1 and 2) and the outer eight carpels (whorls 3 and 4) are decussate, and the positions of whorls 2, 3, and 4 are doubled. The next four carpels (whorl 5) form a tetramerous whorl, followed by a distorted tetramerous whorl (whorl 6) more or less alternating with whorl 5. The next six carpels form two trimerous whorls (whorls 7 and 8). A single carpel is present in whorl 9. Five cursorily studied flowers (a terminal and two lateral flowers and two detached flowers) have 4-6 tepals, and 13-22 carpels (the terminal flower has 4 tepals and 21 carpels; the two lateral flowers have 4 and 5 tepals, and 13 and 19 carpels). The tepals form two decussate pairs, often with one or two of the organ positions of the inner whorl doubled. In all flowers studied, the outer carpels are arranged in the same decussate pattern as the tepals, including double positions. In the inner carpel whorls organ number first increases (to 4, 5, 7, or 9) and then decreases (to 3, occasionally 5).

Kibara (Mollinedioideae, Monimiaceae)

Kibara coriacea - Six sectioned lateral flowers of male thyrsoids (with accessory dichasia) studied have 4 or 6 tepals and 4, 6, 7 or 8 stamens, all decussate (figs. 3*B1*,

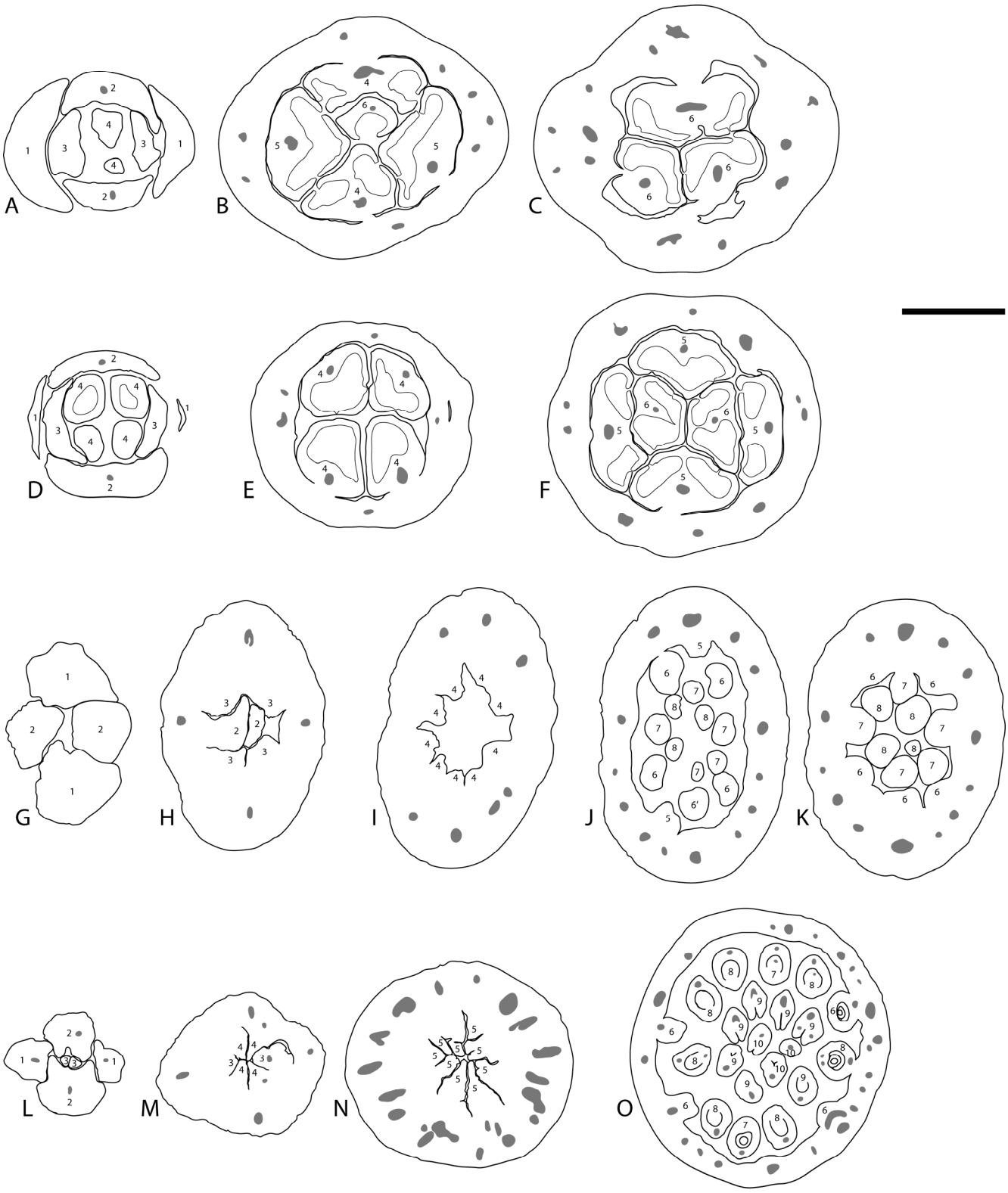

Fig. 18 Mollinedioideae, Monimiaceae, *Wilkiea huegeliana*. Transverse section series of late floral bud, and anthetic flowers. A-C, lateral male flower. A, level of rim of floral cup. B, C, level of androecium. D-F, terminal male flower. D, level of rim of floral cup. E, F, level of androecium. G-K, lateral female flower bud. G-I, level of tepals. J, J, level of gynoecium. L-O, probably terminal female flower. L-M, level of tepals. O, level of gynoecium. Gray: vasculature. Floral organs numbered according to whorls. Bar = 1mm.

16*A*, 16*B*). The odd stamen occupies the center of the flower. All six flowers of a thyrsoid cursorily studied (collection PKE 9325) have a decussate phyllotaxis; the terminal flower has 10 tepals and 10 stamens, and the other flowers have 8 tepals and 6 or 8 stamens.

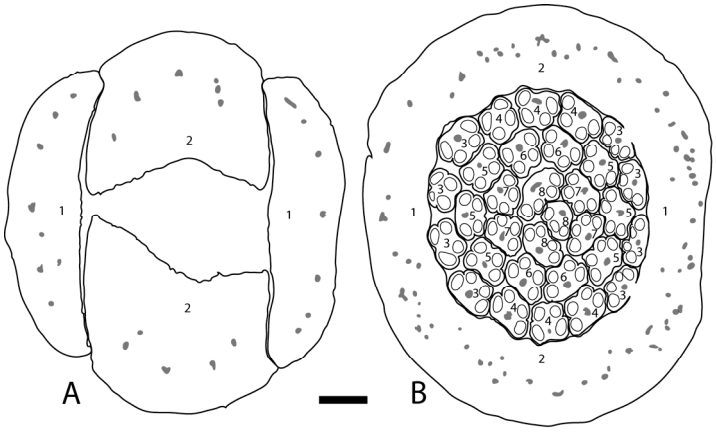

Fig. 19 Mollinedioideae, Monimiaceae, *Austromatthaea elegans*. Transverse section series of late probably lateral male floral bud. A, level of base of tepals. B, level of base of outer stamens. Gray: vasculature. Floral organs numbered according to whorls. Bar = 1mm.

Kibara macrophylla - A probably lateral flower of a female thyrsoid sectioned (fig. 16*C*-16*E*) has 10 tepals, and 22 carpels. Floral phyllotaxis follows approximately fig. 3*E*. Phyllotaxis of the tepals (whorls 1-5) and the outer 10 carpels (whorls 6-8) is decussate. The eight outer carpels (whorls 6 and 7) are in double positions. The inner twelve carpels form three tetramerous whorls (whorls 8-10). Five cursorily studied flowers of two dichasia have 10 or 12 tepals and 17 carpels (terminal flowers), and 10 or 12 tepals and 17, 19, or 20 carpels (lateral flowers). In all flowers, the tepals are decussate. Phyllotaxis of the ten outer carpels is as in the sectioned flower. The inner carpels appear to form one or two whorls with 5 and 2 organs in the terminal flowers, and with 8 and 2 organs in one lateral flower, and one whorl with 7 organs in the two other lateral flowers. A female flower depicted with the SEM shows the arrangement of the carpels in the floral cup with a hyperstigma (fig. 21*D*).

Wilkiea (Mollinedioideae, Monimiaceae)

Wilkiea angustifolia - Inflorescences of the studied collection do not terminate in a flower, but tend to revert to vegetative growth. A male flower sectioned (fig. 17*A*, 17*B*) has 6 tepals, and 4 stamens. Floral phyllotaxis is decussate (fig. 3*B1*). Three cursorily studied male flowers do not differ from the sectioned flower.

A female flower sectioned (fig. 17*C*-17*H*) has 22 tepals, and 12 carpels. Floral phyllotaxis follows approximately fig. 3*E*. The tepals form five decussate pairs (whorls 1-5), and three pairs of double positions (whorls 6-8). The outer eight carpels also form two pairs of double positions (whorls 9 and 10). Thus instead of a transition to a tetramerous whorl after the first whorl with double positions (whorl 6), there is a fourfold repetition of double positions. Only the innermost four carpels (whorl 11) form a tetramerous whorl. Five cursorily studied flowers have 14 (one flower), 18 (three flowers), and 19 (one flower) tepals, and 12 (two flowers), 15 (two flowers) and 17 carpels (one flower). The outer tepals form five decussate pairs, and probably a pair of double positions. The inner tepals appear to be arranged in one or two pairs of double (rarely triple) positions. The carpels of the two flowers with twelve carpels appear to be arranged as in the sectioned flower. The outer carpels of the flower with 17 carpels appear to either form two decussate pairs of two and three, or a 10-merous whorl; the inner carpels appear to form a 6-merous whorl, and there is a single carpel in the center of the flower.

Wilkiea huegeliana - A lateral flower of a male botryoid (fig. 18*A*-18*C*) has 6 tepals and 7 stamens. Floral phyllotaxis is decussate (fig. 3*B1*), including the three stamens in the center of the flower (whorl 6), which form a pair in which one of the positions is doubled. Another male flower sectioned (fig. 18*D*-18*F*) has 6 tepals and 10 stamens. Floral phyllotaxis follows fig. 3*C* (floral diagram fig. 22*L*). The tepals (whorl 1 to 3) and the four outer stamens (whorl 4) are decussate with the stamens in double positions. The inner six stamens form a tetramerous (whorl 5) and a dimerous whorl (whorl 6). Nine other cursorily studied flowers have 4 or 6 tepals, and 6, 7, 8, or 10 stamens. Organ number per flower tends to decrease in the distal portion of the inflorescence (and even the terminal flower has only four tepals and six stamens). In most flowers, floral organs are decussate, with occasionally a whorl of three stamens in the center of the flower. Only in the flower with ten stamens are there two double positions of stamens followed by a tetramerous whorl and two stamens in the center of the flower (floral diagram fig. 22*M*).

A lateral female flower of a botryoid sectioned (fig. 18*G*-18*K*) has 17 tepals and 16 carpels. The 8 outer tepals are decussate (whorls 1-3), whorl 3 with double positions. The subsequent 9 tepals (whorl 4) form a whorl with three double and one triple position. Thus instead of forming a simple tetramerous whorl, the occurrence of multiple positions is repeated. The outer seven carpels appear to form a decussate pattern; the outermost two carpels (whorl 5) form a pair, which is followed by a double position (whorl 6) (fig. 18*J*). The nine inner carpels form penta- and tetramerous whorls (whorls 7 and 8, see fig. 18*J*, 18*K*). Another female flower sectioned (fig. 18*L*-18*O*) has 19 tepals and 23 carpels. The ten outer carpels form three decussate pairs (whorls 1-3) and a pair of double positions (whorl 4). The subsequent ten tepals form a whorl with

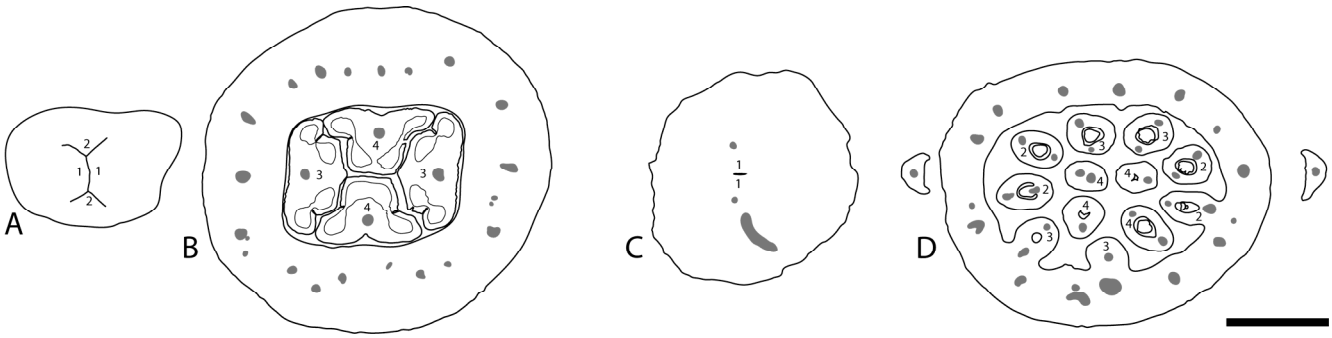

Fig. 20 Mollinedioideae, Monimiaceae, *Steganthera ilicifolia*. Transverse section series of flower, and late floral bud. A, B, male flower. A, level of base of tepals. B, level of androecium. C, D, female floral bud. C, level of tepals. D, level of gynoecium. Gray: vasculature. Floral organs numbered according to whorls. Bar = 1mm.

three double positions and one triple position (whorl 5). Carpel phyllotaxis appears to follow approximately fig. 3*D* (floral diagram fig. 22*N*). The outer four carpels (whorl 6) form two double positions, which are followed by two simple positions (whorl 7), and a 7-merous whorl (whorl 8). This is followed by another 7-merous whorl (whorl 9) and two carpels in the center of the flower (whorl 10). Seventeen cursorily studied flowers (six of which from one botryoid) have 18-20 tepals and 18-36 carpels (the terminal flower has 20 tepals and 35 carpels). Tepals form two to three simple pairs, one pair of double positions, and a whorl of four double and triple positions. Carpels form two decussate pairs of double or triple positions, followed by 4-, 6-, 8-or 12-merous whorls.

Wilkiea longipes – A female flower depicted with the SEM shows the decussate phyllotaxis of the tepals (fig. 21*C*).

Austromatthaea (Mollinedioideae, Monimiaceae)

Austromatthaea elegans - A probably lateral flower of a male thyrsoid sectioned (fig. 19*A*, 19*B*) has 4 tepals and 31 stamens. Floral phyllotaxis follows approximately fig. 3*F* (floral diagram fig. 22*O*). The four tepals form two decussate pairs (whorl 1 and 2). Stamens form multiple positions in a decussate pattern: four stamens in a sector (whorl 3), three stamens (whorls 4 and 5), and two stamens (whorls 6 and 7). Three stamens are in the center of the flower (whorl 8). Seven cursorily studied flowers (four loose flowers from collection PKE 4196 and three from a 3-flowered thyrsoid from collection PKE 9030) have 4 tepals, and 27 (one lateral flower), 28 (three loose flowers), 29 stamens (one lateral flower, one loose flower), and 32 stamens (terminal flower). Floral phyllotaxis is the same in all of them, except in whorl 7 and 8, in which the stamens form either simple or double positions.

A postanthetic female flower cursorily studied has 4 tepals and ca. 230 carpels. Parastichies are not present, which indicates irregular phyllotaxis.

Steganthera (Mollinedioideae, Monimiaceae)

Steganthera ilicifolia - Three male flowers sectioned (collection PKE 4070, 4071, 4074; fig. 20*A*, 20*B*) have 4 tepals, and 2 or 4 stamens. Floral phyllotaxis is decussate (fig. 3*B1*). In a fourth flower (collection PKE 4051), the stamens form a trimerous whorl with a stamen in the center. Two cursorily studied flowers (a terminal and a lateral flower of collection PKE 4074) have both 4 tepals and 8 stamens, all decussate.

A lateral flower of a three-flowered female botryoid sectioned (fig. 20*C*, 20*D*) has 4 tepals, and 12 carpels. Floral phyllotaxis follows approximately fig. 3*C*. The four tepals (whorls 1 and 2) and the eight outer carpels (whorls 3 and 4) are decussate. The organ positions of whorls 3 and 4 are doubled. The 4 inner carpels (whorl 5) form a whorl. Three cursorily studied flowers have 4 tepals, and 11, 15, and 16 carpels. Floral phyllotaxis is similar to that of the sectioned flower, although the number of carpels of whorls 3 and 5 differs. In the flowers with 15 and 16 carpels, the organs of whorl 4 are in triple positions, and there is a whorl of 5 or 6 carpels in the center of the flower. In the flower with 11 carpels, one of the positions of whorl 3 is single, and a whorl of 4 carpels is in the center. Eight cursorily studied fruits (two of which part of an infructescence) have 6-15 carpels (fertilized or not). The terminal fruit has 15 carpels. The lateral fruit has 12 carpels.

Discussion

Diversity of floral phyllotaxis patterns

Spiral floral phyllotaxis

Completely spiral floral phyllotaxis occurs (perhaps with the exception of Siparunaceae) at least partly in all families (and subfamilies) studied: Gomortegaceae, Atherospermataceae (*Daphnandra repandula*), Monimioideae (all), Mollinedioideae (*Hortonia*; Endress 1980a; some female flowers of *Hedycarya angustifolia*; this study). In all cases the flowers are Fibonacci spiral; Lucas spiral flowers were not found. In spiral flowers, the change from vegetative decussate to spiral phyllotaxis occurs in two ways: (1) in the terminal flower of an inflorescence, the change occurs at the transition from the uppermost bracts of the inflorescence axis to the outermost floral organs, which may still be almost opposite; (2) in lateral flowers, the first two tepals have a transverse position, as expected from the prophylls. There are also flowers in which the transition

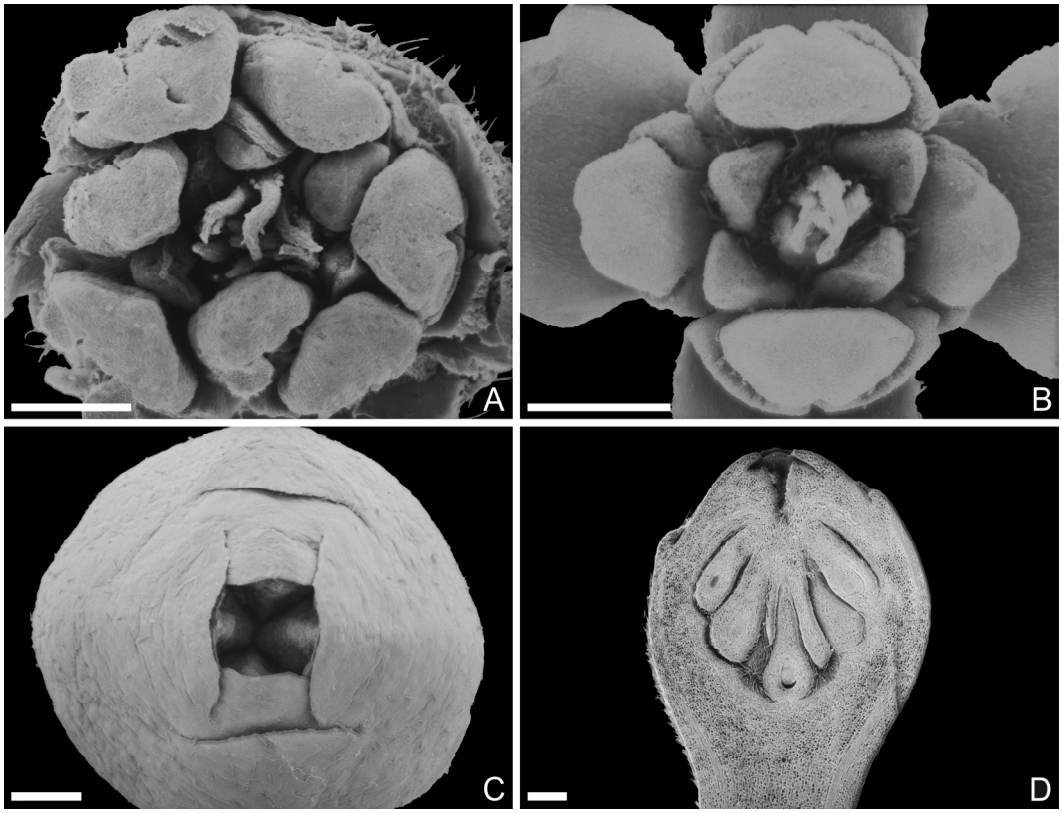

Fig. 21 SEM micrographs of flowers. A, B, Atherospermataceae. C, D, Monimiaceae. A, *Daphnandra repandula*, anthetic flower, perianth removed. B, *Daphnandra micrantha*, anthetic flower. C, *Wilkiea longipes*, anthetic female flower. D, *Kibara macrophylla*, longitudinal section of anthetic female flower. Bar = 0.5mm.

from whorled to spiral occurs only at the transition from the perianth to the stamens or carpels, such as Atherospermataceae (*Doryphora aromatica*), Siparunaceae (male flowers of *Glossocalyx*, female flowers of *Siparuna thecaphora*), Mollinedioideae (male flowers of *Levieria acuminata* and *Xymalos*). In these flowers the onset of sporophyll initiation may be preceded by a long plastochron, which may reconstitute a circular dome-shaped floral apex. This, in turn, would create a Fibonacci spiral phyllotaxis (see also Eupomatiaceae; Endress 2003; or the model of Reinhardt et al. 2003; see also Jönsson et al. 2006).

Simple whorled floral phyllotaxis

Simple whorled floral phyllotaxis, i.e., with uniformly isomerous whorls, is present in the study group only in the form of dimerous whorls. Thus it represents a simple continuation of the decussate phyllotaxis of the leaves and the floral subtending bracts in the inflorescence. It was found in Mollinedioideae (male flowers of *Kibara coriacea*, *Steganthera ilicifolia*, *Wilkiea angustifolia*, some male flowers of *W. huegeliana*, and some female flowers of *Xymalos*), and also in Siparunaceae (some male flowers of *Siparuna thecaphora*). The tetramerous flowers of *Dryadodaphne trachyphloia*, and *Daphnandra micrantha* (Atherospermataceae) begin with two dimerous whorls, and are therefore, strictly speaking, not simple whorled from the beginning (see below). Thus simple whorled floral phyllotaxis is not so common in pluricarpellate families of core Laurales. In contrast, it is pervasive in unicarpellate core Laurales, where, in addition, the floral whorls are not dimerous, but largely trimerous in Lauraceae (e.g., Mez 1889; Singh and Singh 1985; Hyland 1989; Rohwer 1993; Buzgo et al. 2007), and trimerous, tetramerous, and pentamerous in Hernandiaceae (Kubitzki 1969; Endress and Lorence 2004; Kimoto and Tobe 2008). Tetramerous flowers of Lauraceae and Hernandiaceae also begin with two dimerous whorls (Endress 1987; Endress and Lorence 2004) (see below).

Complex whorled floral phyllotaxis

The diversity in complex whorls is the most striking feature in the floral phyllotaxis in pluricarpellate families of core Laurales. These flowers do not have isomerous whorls but merism increases or decreases once or several times between whorls. An increase in merism comes about in that at the place of an expected single organ two or even more collateral organs are formed (double or multiple positions). Double or multiple positions are a means of regulating organ number by flexibility of merism per whorl, in contrast to the number of whorls as in flowers with simple whorled phyllotaxis. Double or multiple positions also occur in other basal angiosperms (e.g., Nymphaeales; Endress 2001; Annonaceae; Endress 1987; Leins and Erbar 1996; Aristolochiaceae; Leins and Erbar 1985), and in basal eudicots, although double positions have not always been noticed as such in the older literature (e.g., Papaveraceae; Murbeck 1912; Ranunculaceae; Schöffel 1932). Double or

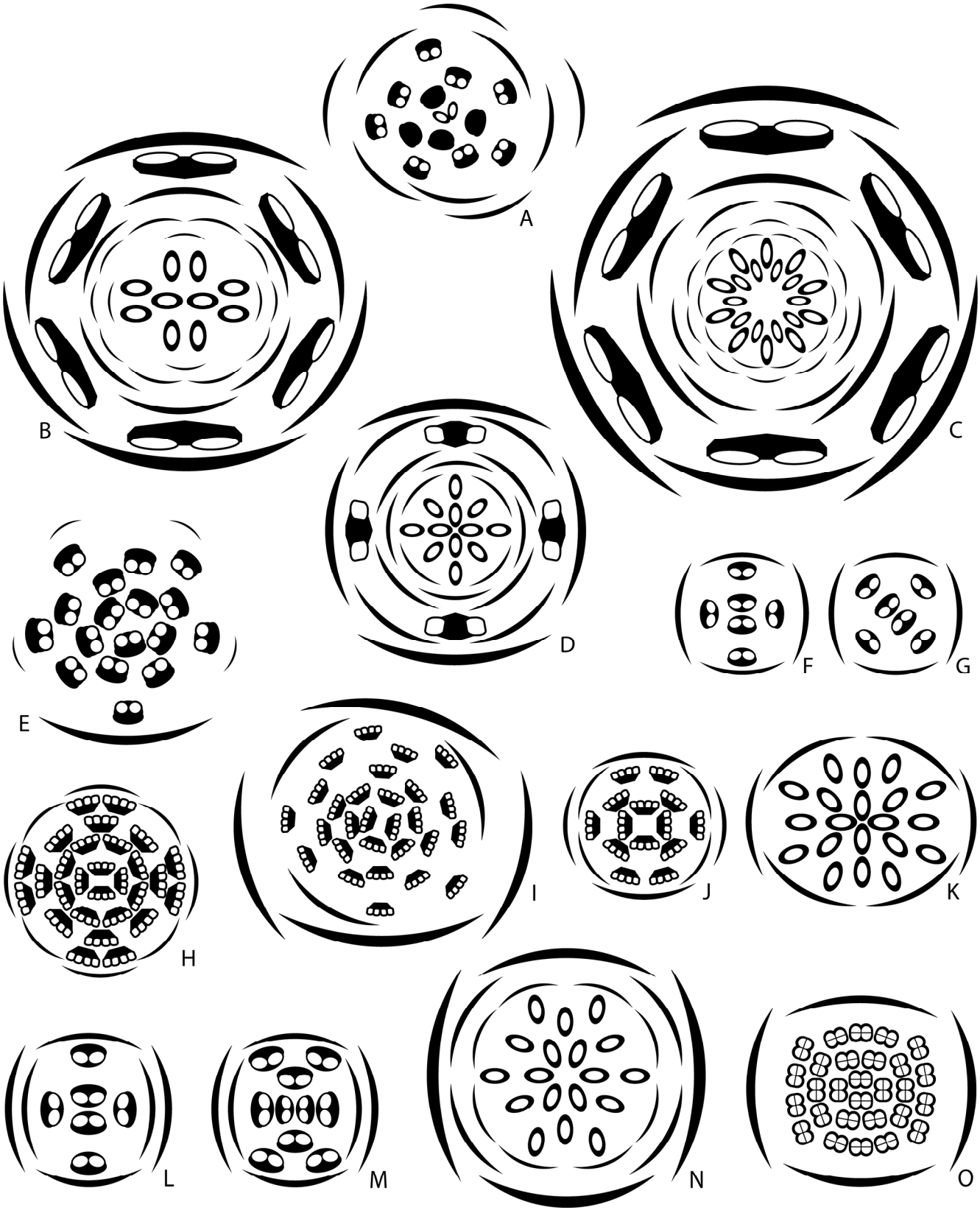

Fig. 22 Floral diagrams. A, *Gomortega keule*. B, *Doryphora sassafras*, terminal flower. C, *Doryphora sassafras*, lateral flower. D, *Dryadodaphne trachyphloia*. E, *Glossocalyx longicuspis*, male flower. F, G, *Siparuna thecaphora*, male flowers. H, *Hedycarya angustifolia*, male flower. I, *Levieria acuminata*, male flower with Fibonacci spiral phyllotaxis. J, *Levieria acuminata*, male flower with whorled phyllotaxis. K, *Levieria acuminata*, female flower. L, *Wilkiea huegeliana*, male flower with few organs. M, *Wilkiea huegeliana*, male flower with numerous organs. N, *Wilkiea huegeliana*, female flower. O, *Austromatthaea elegans*, male flower.

multiple positions most commonly occur at the transition from the perianth to the androecium, associated with a decrease in organ size (as in Annonaceae; Leins and Erbar 1996; or as in a number of eudicots, reviewed by Endress 1987, 1994; Ronse De Craene and Smets 1993a,b) but they may also occur earlier, within the perianth (this study; Endress 1994, 2001; Blarer et al. 2004), or later, within the androecium or at the onset of the gynoecium (this study). The term „dédoublement" was used by earlier authors (e.g., De Candolle 1813), which implies the splitting of a primordium into two. However, such a developmental splitting does not occur. What can be observed is simply a replacement of one organ by two collateral organs. This takes place because the organs are narrower than those of the preceding whorl. Therefore we prefer the term double position instead of dédoublement. A special instance in which double positions are common is in tetramerous flowers of many angiosperms. There the flower commonly begins with two dimerous whorls (whorl 1 and 2). The next four organs are two pairs of double positions (whorl 3). They alternate with the four organs of the first two whorls. The four organs of whorl 4 again alternate with those of whorl 3. Thus the four organs of the two double positions of whorl 3 establish tetramery of the subsequent whorls. Examples among eudicots are Brassicales (Endress 1992; Ronse De Craene and Smets 1996) or Caryophyllales (Ronse De Craene and Smets 1996). In the study group this specific pattern is not common; it occurs in *Dryadodaphne* (Atherospermataceae). Among other Laurales, it is known from tetramerous Lauraceae (Endress 1987) and Hernandiaceae (Endress and Lorence 2004) (see above).

It is of special interest that double or multiple positions are very common in our study group and the site of double positions is considerably flexible. As in other plants they often occur at the beginning of the androecium (*Daphnandra micrantha*, *Dryadodaphne trachyphloia*, *Austromatthaea elegans*, some male flowers of *Wilkiea huegeliana*). However, in Atherospermataceae and Mollinedioideae double positions also occur in the inner part of the perianth, in Mollinedioideae also in various parts of androecium and gynoecium. An unusual, and probably unrecorded pattern is the repetition (propagation) of decussate whorls with double (or multiple) positions, in which, therefore, the transition to a tetramerous whorl in perianth and gynoecium is delayed (female flowers of *Levieria acuminata*, *Steganthera ilicifolia*, and *Wilkiea huegeliana*. In more complex patterns hexa- or octomerous whorls may result. Hexamerous whorls may be formed after a dimerous whorl with two double positions, followed by a simple dimerous whorl (male flowers of *Atherosperma moschatum*, some female flowers of *Wilkiea huegeliana*. Octomerous whorls may be formed either after a tetramerous whorl of four double positions (male flowers of *Hedycarya angustifolia*, female flowers of *Wilkiea angustifolia*), or after two tetramerous whorls (some female flowers of *Hedycarya angustifolia*). Also previously unrecorded are asymmetrical transitions, in which a double position occurs only in the radius of one organ of a decussate organ pair. In the sectioned lateral flower of *Doryphora sassafras* the two last trimerous whorls of staminodes (whorl 6 and 7) have each a double position in the median plane (fig. 6*F*-6*H*), which results in an octomerous whorl followed by a decamerous whorl by further double positions. In female *Tambourissa purpurea* the whorls change from dimerous to hexamerous by a similar asymmetrical occurrence of double positions.

In flowers with complex whorls, the number of floral organs per whorl decreases toward the center of the flower, as discussed by Endress (1987) for other taxa. This may occur in a regular way (by whorls of similar symmetry, e.g., 8 → 4, in female flowers of *Wilkiea angustifolia*) or in an irregular way (e.g. 4 → 3, in female flowers of *Levieria acuminata*). Both regular and irregular decrease may even occur in the same species (e.g., *Levieria acuminata*).

Irregular floral phyllotaxis

Irregular phyllotaxis is found in flowers with numerous reproductive organs in Mollinedioideae (female flowers of *Austromatthaea elegans* and *Tambourissa ficus*). In such female flowers there is an extensive decrease in size of the organs at the transition from the perianth to the gynoecium. For instance, in *Austromatthaea* 15-17 carpels are positioned in the sector of a single tepal. This decrease in size of the organs with regard to the size of the floral apex appears to cause a loss of order of arrangement of the carpels (see also Endress 2006). As a rule, irregular phyllotaxis does not appear to be linked to an absolute number of organs above which order would be lost, but to a high number relative to a genus: *T. ficus* (2000 carpels; Lorence 1985), *Austromatthaea* (230 carpels; this study) are irregular.

Changes in phyllotaxis patterns within flowers

Not only is there a great diversity of floral phyllotaxis patterns in core Laurales, but there may be even more than one pattern in a single flower. A transition from whorled to spiral occurs in some Atherospermataceae, Siparunaceae, and Monimiaceae. However, the reverse transition, from spiral to whorled phyllotaxis, was not observed, although such a phyllotaxis change is present in many eudicots, in which the prophylls and the sepals are initiated in a spiral sequence, and the petals, stamens, and carpels in whorls (Hirmer 1931; Endress 1987).

Similarly, there are transitions from simple whorled (decussate) phyllotaxis to complex whorled phyllotaxis at the onset of all flowers with complex whorled phyllotaxis. In some flowers the perianth is decussate and the complex whorls are restricted to the fertile organs (*Dryadodaphne trachyphloia*, some male *Siparuna thecaphora*, male flowers of *Wilkiea huegeliana*, *Austromatthaea elegans*), but in others complex worls begin in the perianth (*Daphnandra micrantha*, *Atherosperma moschatum*, *Hedycarya angustifolia*, *Levieria acuminata*, female flowers of *Wilkiea angustifolia*, *W. huegeliana*, *Kibara macrphylla*, and *Steganthera ilicifolia*). Transition from complex whorls to simple whorls is present in all flowers with complex whorls: when whorls of higher merism are initiated (almost all flowers with complex whorls), or merism decreases towards the center of the flower so that the phyllotaxis is again decussate (*Austromatthaea*).

Transition from simple whorled phyllotaxis to irregular phyllotaxis is present in female flowers of *Austromatthaea*, and appears to be due to the strong difference in size between the tepals and the carpels. Such a difference could be present in flowers of *T. ficus* as Lorence (1985) mentions only 6-8 lobes (corresponding to tepals) at the floral orifice.

Floral phyllotaxis and organ number

Flowers with few organs (less than 12 organs) tend to have decussate phyllotaxis, such as male flowers of *Siparuna thecaphora* (10 or 11 organs), *Kibara coriacea* (8-12 organs), *Wilkiea angustifolia* (10 organs), *Steganthera ilicifolia* (8 or 9 organs), and some female flower of *Xymalos monospora* (3-7 organs). However, the androecium of male flowers of *X. monospora* (3-15 stamens) has spiral phyllotaxis.

Flowers with numerous organs (more than 100 organs) tend to have irregular phyllotaxis: female flowers of *Tambourissa ficus* (ca. 2000 carpels**;** this study; Lorence 1985) or *Austromatthaea elegans* (ca. 230 carpels; this study).

In flowers with an intermediate number of organs (between 15 and 100 organs), no simple correlation between organ number and floral phyllotaxis is apparent. In *Daphnandra*, more organs are present in species with spiral phyllotaxis (*D. repandula*, 32-42 organs), than in species with complex whorled phyllotaxis (*D. micrantha*, 19-25 organs). However, in *Doryphora*, the reverse is true, fewer organs are present in species with spiral phyllotaxis (*D. aromatica*, 26-29 organs), than in species with complex whorled phyllotaxis (*D. sassafras*, 46-77 organs).

Within the species for which different phyllotaxis occurs in flowers of the same sex (female flowers of *Hedycarya angustifolia*, and male flowers of *Levieria acuminata*), there is a tendency for flowers with higher organ number (terminal male flowers in *L. acuminata*) to have spiral phyllotaxis, and flowers with lower organ number (lateral male flowers in *L. acuminata*) to have complex whorled phyllotaxis. The presence of spiral and whorled flowers in the same species is also known from Winteraceae (*Drimys winteri*; Doust 2001) and Ranunculaceae (*Actaea spicata*; Schöffel 1932). In *Drimys*, as in *H. angustifolia* and *L. acuminata*, lateral flowers tend to have whorled phyllotaxis, whereas terminal flowers tend to have spiral phyllotaxis, correlated with higher organ number, and probably a more rounded floral apex shape at floral organ initiation (Doust 2001); also other irregularities occur (Erbar and Leins 1983).

In species with an intermediate number of organs and complex whorled floral phyllotaxis, three cases may be distinguished: (1) flowers with relatively low number of organs (12-18 organs, male flowers of *Laurelia sempervirens* and *Wilikiea huegeliana*). Within flowers with relatively low number of organs, flowers with below average number of organs (lateral flowers in *L. sempervirens*, but terminal flowers in *W. huegeliana*) comprise decussate pairs and only one pair of double positions, whereas in flowers with above average number of organs (terminal flowers in *L. sempervirens*, but lateral flowers in *W. huegeliana*), the pair of double positions is followed by a tetramerous whorl. (2) Flowers with a relatively high number of organs (19-100 organs, most whorled Atherospermataceae, and female flowers of Mollinedioideae). Within flowers with a relatively high number of organs, flowers with above average number of organs (terminal flowers), two organs can be found where only one would be expected (inner whorls of the male flowers of *Austromatthaea elegans*), or three or four organs may be found where only two would be expected (outer whorl of carpels in *W. huegeliana*). Similarly, in flowers with below average number of organs (lateral flowers, accessory flowers), only one organ may be found where two would be expected (outer stamen whorl of male flowers of *Hedycarya angustifolia* and *Levieria acuminata*), which, in turn, tends to decrease the merism of the inner whorls. In flowers with below average number of organs, a direct change in merism can also occur (from 4- to 3-merous whorls in staminodes and carpels in accessory flowers of *Daphnandra micrantha*). In flowers of both sexes of *Tambourissa purpurea*, and female flowers of *Xymalos monospora*, number of whorls increases in flowers with above average number of organs (terminal flowers), but merism remains constant. (3) Flowers with more complex organ number variation. In *Doryphora sassafras* more stamens but fewer staminodes are present in terminal flowers than in lateral flowers. Stamens are arranged in complex whorls in the terminal flowers and in simple (trimerous) whorls in the lateral flowers. Staminodes are arranged in complex whorls in both lateral and terminal flowers, however, there are three 10-merous whorls of staminodes in lateral flowers, and only one in terminal flowers.

No correlation between organ number and spiral phyllotaxis was found. Organ munber ranges from 5 (some male flowers of *Xymalos*) to 59 (some male flowers of *Peumus*). Within a species, in flowers with more organs (terminal flowers in most taxa, lateral flowers in *Palmeria gracilis*), organ number per organ series appears in higher Fibonacci numbers (8, 13) than in flowers with fewer organs (3, 5, 8).

In flowers of both sexes of *Palmeria gracilis*, and male flowers of *Hedycarya huegeliana*, terminal flowers have fewer organs than lateral flowers. This uncommon behavior could indicate that terminal flowers may not have more organs as a rule, but simply be more plastic than lateral flowers. However, we studied only a few inflorescences of each taxon, so this requires further studies in suitable species.

Phyllotaxis and floral shape

Flowers with a narrow, tubular floral cup (with few organs: 8-12 inserted at the same level) have simple whorled floral phyllotaxis (male flowers of *Siparuna thecaphora*, *Kibara coriacea*, *Wilkiea angustifolia*, *Steganthera ilicifolia*). Flowers with a tubular floral cup (with a higher number of organs: 13-99) commonly have complex whorled phyllotaxis, but whorl merism tends to change only once (fig. 3*C*; *Daphnandra micrantha*, *Dryadodaphne trachyphloia*, male and female flowers of *Tambourissa purpurea*, and male flowers of *Wilkiea*

huegeliana). Flowers with a flat base on which organs lie, but are still enclosed in a floral cup, tend to have multiple double positions and tetramerous whorls in the center of the flower (*Kibara macrophylla*, *Wilkiea angustifolia, Wilkiea huegeliana, and Steganthera ilicifolia*). Flowers with a flat base on which organs lie, and are not enclosed in a floral cup, tend to be have few double positions, and hexa- and octomerous whorls (*Atherosperma moschatum*, *Hedycarya angustifolia*, *Levieria acuminata*).

The more complex patterns (6- or 8-merous whorls) appear to be present in flowers in which the widening of the floral apex is not restricted by the floral cup. There is thus a trend in more open flowers to have organs arranged in whorls or series of higher organ number than in more closed flower. It is also among species with a flat floral base, that there are flowers of the same sex with both spiral and whorled phyllotaxis (female flowers of *H. angustifolia*, and male flowers of *L. acuminata*).

No specific type of floral construction appears to be correlated with spiral phyllotaxis. The floral base can be convex and the floral cup almost absent (male flowers of *Xymalos monospora*), almost flat (male flowers of *Palmeria gracilis*, and *Peumus boldus*), or concave (*Gomortega keule*), or even "closed" and urceolate (female flowers of *Siparuna thecaphora* and *Palmeria gracilis*).

Phyllotaxis in unisexual and bisexual flowers

In the few taxa of multicarpellate core Laurales with bisexual flowers (*Gomortega*, *Daphnandra*, *Doryphora*, *Dryadodaphne*, and *Hortonia*), spiral phyllotaxis is dominant; however, bisexual flowers with complex whorls are present in Atherospermataceae (*Daphnandra*, *Doryphora*, and *Dryadodaphne*).

In most taxa studied, phyllotaxis of male and female flowers differs. This difference is correlated either with different organ numbers (and perhaps shapes and sizes) or with floral construction, or both. In flowers in which the floral cup more or less completely encloses the reproductive organs (*Siparuna thecaphora*, *Tambourissa purpurea*, *Kibara macrophylla*, *Wilkiea angustifolia*, *W. huegeliana* and *Steganthera ilicifolia*), male flowers tend to have fewer organs, and tend to be more narrow than female flowers. Female flowers are also more variable in floral merism (whorls of different merism are observed in the same part of female flowers of *K. macrophylla*, *W. angustifolia*, *W. huegeliana* and *S. ilicifolia*). In *Austromatthaea elegans*, perianth phyllotaxis is the same in male and female flowers, but there are many more carpels in female flowers than there are stamens in male flowers, so that the phyllotaxis is whorled with decussate multiple positions in male flowers and irregular in female flowers.

Floral phyllotaxis and hyperstigma

A hyperstigma is present in species of *Tambourissa*, *Kibara*, *Wilkiea*, *Hennecartia* (Endress 1979b, 1980b, Endress and Igersheim 1997), and *Faika* (Philipson 1993). Such flowers have a narrow canal formed by the exit of the floral cup lined with highly reduced tepals. Flowers with a hyperstigma all have complex whorled phyllotaxis. Within the canal, the number of tepals at a given level is small, which restricts phyllotaxis variability. All flowers with a hyperstigma have an increased number of tepals by double positions (*Tambourissa*, *Kibara*, and *Wilkiea*; Endress 1980b). In contrast, most male flowers of taxa with a hyperstigma do not have double positions of tepals (male flowers of *Tambourissa purpurea* are an exception), and their phyllotaxis is either simple whorled (decussate, *Kibara*, *Wilkiea angustifolia*) or complex whorled (*Tambourissa*, *Wilkiea huegeliana*). Whorled female flowers of Monimioideae without a hyperstigma, as in *Xymalos*, *Hedycarya*, *Levieria*, *Austromathaea*, and *Steganthera*, tend to have fewer tepals than flowers with a hyperstigma, and to not have double positions in the perianth (except for *Levieria* and *Hedycarya*). *Grazielanthus* (Peixoto and Pereira-Moura 2008) is reported to have secretory tepals, but only four tepals are mentioned.

Floral monosymmetry

Floral monosymmetry is uncommon in Laurales, where it is restricted to *Glossocalyx longiscuspis*, *Steganthera stevensii* (Takeuchi 2001), and some Gyrocarpoideae of Hernandiaceae (Kubitzki 1969). In *S. stevensii*, zygomorphy of the lateral flowers appears to be due to the fusion of the floral cup with the subtending bract; terminal flowers have two large appendages, probably as the result of the fusion of the floral cup with two bracts preceding the terminal flower (terminal flowers have disymmetry). In *Glossocalyx*, the "enlarged tepal" may also be derived from a subtending bract. Arguments in favor of a subtending bract origin are: (1) no distinct subtending bract was found in our material. (2) the vasculature of the enlarged tepal is distinct from the other tepals, and fuses only with that of two stamens and joins the other bundles to form a stele only in the peduncle (the vasculature of the other tepals ramify just below their base). Arguments against such an origin are: (1) subtending bracts are usually minute and deciduous in Siparunaceae (Renner and Hausner 2005) which would make them easy to miss, especially on herbarium material. (2) the occurrence of flowers with two, three, or four enlarged tepals suggests that these organ have the same identity (see illustration in Fouilloy 1974), although one tepal always appears to be larger than the others. (3) two pairs of tepals enlarge strongly during the development of the wind dispersed fruits of *Gyrocarpus* (Kubitzki 1969); tepal enlargement is thus present in Laurales. More observation on pickled or fresh material is needed to reach a conclusion about the origin of the enlarged "tepal" in *Glossocalyx*. Especially interesting would be to compare tepal differentiation in lateral and terminal flowers.

Inner staminodes: structure and function

Inner staminodes, sterile stamen-like organs between stamens and carpels in bisexual flowers, are found in several families of basal angiosperms (Endress 1984). In basal Laurales (Calycanthaceae) inner staminodes are always present (Friis et al. 1994; Crepet et al. 2005; Staedler et al. 2007). Among core Laurales, inner staminodes (often nectariferous) are present in *Gomortega* (Reiche 1896), Atherospermataceae (Schodde 1969), and in

Hortonia of Mollinedioideae (Endress 1980a), and further in Lauraceae (e.g., Mez 1898; Rohwer 1993; Hyland 1989; Buzgo et al. 2007) and Hernandiaceae (Kubitzki 1969; Endress and Lorence 2004). Staminodes are also present in female flowers of *Peumus boldus*. In Atherospermataceae, inner staminodes are persistent and appear to play a role in the closure of the floral cup after anthesis and recurving at fruit maturity for differential release of fruitlets (*Doryphora*, and *Laurelia philippiana*) (Schodde 1969). A similar function for apparently homologous organs has been described in Calycanthaceae (Staedler et al. 2007), which may be either a synapomorphy or a plesiomorphy at the order level, retained only in Calycanthaceae and Atherospermataceae. Number of (inner) staminodes is low in *Gomortega* (2-4; this study; Brizicky 1959; Heo et al. 2004), *Peumus* (10-13; this study), and *Hortonia* (2-7; Endress 1980a), and in these genera they do not play a role in fruit development or dispersal (Doweld 2001; Heo et al. 2004; Romanov et al. 2007). The velum of Siparunaceae (Endress 1980b) and the inferior ovary of Gomortegaceae may have evolved to compensate for the loss of the protective function of the persisting staminodes during fruit development.

Carpellodes: structure and function

Capellodes are sterile carpel-like organs. They are present in female flowers between tepals and carpels in some taxa studied (*Palmeria gracilis*, *Tambourissa purpurea*, and *Hedycarya angustifolia*). In male flowers, carpellodes were not found.

In *Tambourissa purpurea*, the sterile organs were previously considered to be all tepals (Endress 1980b). However, it is possible to distinguish two types of organs from their shape (small knob-like organs vs. organs with a stigma-like surface), epidermis (normally staining vs. strongly staining), vascularisation (absent vs. present). The outer sterile organs are thus considered to be tepals and the inner ones carpellodes. Nevertheless, there is holocrinous secretion at the mouth of the floral pore also involving part of the outer tepals at anthesis (Endress 1980b). Thus the hyperstigma is made up of tepals and carpellodes. Carpellodes form whorls together with carpels but not with tepals. Carpellodes also occur in flowers without a hyperstigma such as in *Hedycarya* (*H. angustifolia*; this study, and *H. arborea*; Sampson 1969a). In both species, they are in two whorls at the periphery of the gynoecium. In *Hedycarya*, carpellodes may have a role in floral display, as they increase the size of a probably glistening attractive surface, and may play a role in pollinator reward. In the flowers of *Kibara* and *Wilkiea* there are also secretory organs between the outer tepals and the carpels (Endress 1980b). However, these organs are separated from the carpels by an organ-free portion of the floral cup, and fall off with the tepals as a calyptra after anthesis. Both observations indicate a tepal nature for these secretory organs. In Calycanthaceae, the inner staminodes have sometimes been referred to as potential carpellodes (Hiepko 1965), but such identity is unlikely (Staedler et al. 2009). Furthermore, organs that are unambiguously carpellodes are present in some flowers of *Idiospermum australiense* (Staedler et al. 2009). Carpellodes also appear to be present in the calycanthaceous fossil *Jerseyanthus* (Crepet et al. 2005).

Irregularities in organ sequence

Irregularities in organ sequence refer to (1) reversed organ sequence along the ontogenetic spiral in spiral phyllotaxis and whorls with two kinds of organs in whorled phyllotaxis; (2) missing organs along the ontogenetic spiral in spiral phyllotaxis or in a whorl in whorled phyllotaxis. The first case occurs in Atherospermataceae (*Doryphora aromatica*) and in Monimiaceae (female flowers of *Palmeria gracilis*, female flowers of *Tambourissa purpurea*, some female flowers of *Hedycarya angustifolia*). The organ sequence irregularities always occur at the transition between sterile organs (staminodes in *D. aromatica*, carpellodes in *T. purpurea* and *H. angustifolia*) and the carpels. Such irregularities are also present at the transition between the staminodes and carpels in Calycanthaceae (Staedler et al. 2007). As noted by Staedler et al. (2007), they were also described at the level of inflorescences in Asteraceae (between bracts, ray flowers and disk flowers; Hirmer 1931, Bachmann 1983; Battjes and Bachmann 1996; Battjes and Prusinkiewicz 1998). These irregularities may be due to the fact that at the time of initiation, the floral apex is large in size compared to primordium size, and that organ identity would depend more on the immediate sectorial neighborhood than the position on the ontogenetic spiral in spiral flowers (*D. aromatica*, *H. angustifolia*), and than the position of the whorl in whorled flowers (*T. purpurea*).

The second case is present in a studied female flower of *Palmeria gracilis*, and of *Hedycarya angustifolia*. There is a missing position in the ontogenetic spiral in the sectioned female flower of *Palmeria gracilis*. The missing position is almost on the same radius as the last tepal initiated, which suggests that the last tepal primordium inhibited the initiation of a carpel in his vicinity, in accordance with an auxin sink model (Reinhardt et al. 2003). In *Hedycarya angustifolia*, there is a carpellode missing in whorl 6, probably due to space constraints. This appears to be the opposite phenomenon to occasional organ doubling or tripling as in female flowers of *Tambourissa purpurea*, *Wilikiea huegeliana*, and *Steganthera ilicifolia*.

Systematic aspects

Gomortegaceae

Earlier reports on floral structure of *Gomortega* are conflicting regarding phyllotaxis (whorled, tetramerous; Mez 1889; spiroidal; Reiche 1896; Leinfellner 1968; spiral; Stern 1955) or do not consider phyllotaxis at all (Buchheim 1958; Brizicky 1959). In the most recent account on floral phyllotaxis based on a review and new observations (Kubitzki 1993a) it is described as „neither clearly spiral nor clearly trimerously whorled, but rather intermediate between both conditions“. Thus the situation was uncertain to date. In the present study we clearly show a regular spiral phyllotaxis in both terminal and lateral flowers. Only the

two innermost divergence angles in the center of a flower strongly differ from the Fibonacci divergence angle, but this is not uncommon also in other families (e.g. Monimiaceae; this study; Calycanthaceae; Staedler et al. 2007).

Atherospermataceae

At genus level floral phyllotaxis is either whorled (*Atherosperma*, *Dryadodaphne*, and *Nemuaron* (this study; Schodde 1969) or spiral and whorled phyllotaxis coexist (spiral in *Laurelia novae-zelandiae*; Sampson 1969b; but worled in *L. sempervirens*; this study; spiral in *Daphnandra repandula*, but whorled in *D. micrantha*; this study; spiral in *Doryphora aromatica*, but whorled in *D. sassafras*; this study; and to make the situation even more unstable, Schodde, 1969, found whorled flowers in *Doryphora aromatica*). Interestingly, there is no genus with exclusively spiral phyllotaxis. Among the whorled flowers, *Atherosperma*, *Dryadodaphne*, and *Laurelia* are dimerous/tetramerous (this study), whereas *Nemuaron* and *Doryphora* fluctuate between trimerous and tetramerous (Schodde 1969). „Sub-spiral“ phyllotaxis, as mentioned (without definition) by Schodde (1969) for some taxa, was not found in our material. Thus, of the two major clades of the family (Renner et al. 2000), one fluctuates between whorled and spiral, and the other is consistently whorled (except for *Laurelia*, which also fluctuates between whorled and spiral).

Siparunaceae

Flowers with completely spiral phyllotaxis were so far not found in Siparunaceae. Male flowers of *Glossocalyx* are whorled in the perianth and spiral in the androecium (this study). In *Siparuna thecaphora* male flowers are whorled (dimerous), whereas female flowers are whorled only in the perianth but spiral in the gynoecium (this study). Male flowers of *S. aspera* are also whorled (dimerous) (Bello et al. 2002). The occurrence of irregular phyllotaxis was indicated for species with a high organ number (Renner and Hausner 2005). Floral organ numbers show striking intraspecific variability, with up to 72 stamens and up to 35 carpels (Renner and Hausner 2005).

Monimiaceae

Monimioideae and *Hortonia*, which is sister to all other Mollinediodieae, have spiral floral phyllotaxis. Mollinedioideae form a basal grade and a number of genera in an unresolved trichotomy (Renner 2004). Beginning in the second clade of the basal grade floral phyllotaxis becomes highly variable. *Tambourissa* has complex whorls, or phyllotaxis is irregular, the latter especially in flowers with excessively numerous organs (*T. ficus* has with up to 2000 stamens and carpels; Lorence 1985), and in *Ephippiandra* simple dimerous whorls (Perkins 1925) and complex whorls occur (Lorence 1985). *Hedycarya* and *Levieria* have both spiral and complex whorled patterns. Of the three clades forming the mentioned trichotomy, *Steganthera* and *Austromatthaea* have simple whorls, complex whorls and (in *Austromatthaea*, with numerous organs) also irregular patterns, and in *Wilkiea* simple dimerous whorls and complex whorls occur; the Neotropical clade of *Mollinedia* and relatives has not been studied.

Evolution of floral phyllotaxis in Laurales

The basal state of floral phyllotaxis in Laurales is equivocal for the perianth (spiral or whorled) and spiral for the androecium (Endress and Doyle 2007). Calycanthaceae, which are sister to all other Laurales, have consistently spiral flowers (Staedler et al. 2007). Spiral flowers were retained in Gomortegaceae (this study) and in the basal clades of Monimiaceae (Monimioideae and *Hortonia*), whereas in the higher Mollinedioideae lability between spiral and whorled patterns and, with an excessive increase of stamens or carpels (*Austromatthaea*, species of *Tambourissa*), also irregular phyllotaxis evolved (this study). In Siparunaceae flowers are whorled in the perianth and androecium but spiral in the gynoecium (this study) but may also be irregular (Renner and Hausner 2005). In Atherospermataceae, whorled flowers are predominant, but in three genera (from both major clades) lability between whorled and spiral phyllotaxis occurs. In Hernandiaceae and Lauraceae spiral flowers are not known; in all extant species studied, phyllotaxis is whorled (Mez 1889; Kubitzki 1969; Hyland 1989; Endress and Lorence 2004; Buzgo et al. 2007; Kimoto and Tobe 2008), except for a few Lauraceae (species of *Lindera* and *Litsea*) that have lost their perianth and have an irregular phyllotaxis (Endress 1990). In floral fossils ascribed to Lauraceae phyllotaxis is also whorled (trimerous) (*Mauldinia*; Drinnan et al. 1990; Viehofen et al. 2008; *Perseanthus*, Herendeen et al. 1994; *Neusenia*, Eklund 2000; *Lauranthus*, Takahashi et al. 2001; *Potomacanthus*, von Balthazar et al. 2007).

Conclusions

Because floral phyllotaxis is diverse, in some genera of Atherospermataceae and Monimiaceae, even at species level, floral phyllotaxis evolution is expected to be complex. A realistic picture of floral phyllotaxis evolution in these families would require a very broad taxon sampling down to species or maybe even population level. Nevertheless, from the distribution of this diversity it can be concluded that lability of phyllotaxis is unusually extensive in core Laurales, and evolutionary oscillations between spiral and whorled patterns may be frequent in certain genera or species. Another approach would be to focus on species found to be especially labile in the present study and to carry out developmental studies to investigate conditions leading to different patterns in more detail.

The change from simple whorled phyllotaxis to complex whorled phyllotaxis and vice-versa appears to be linked to organ number and floral cup constraint. The change from complex or simple whorled phyllotaxis to spiral phyllotaxis within a flower as in Mollinedioideae is correlated with only weakly developed floral cups (flat or convex floral bases). In contrast the change from spiral to whorled phyllotaxis within a flower was not found, suggesting that this change is developmentally difficult.

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GENERAL SUMMARY

The present doctoral dissertation provides new results on the comparative floral structure in phylogenetically basal angiosperms. Five families of the order Laurales were studied: Calycanthaceae, which are sister to all other families ("core Laurales"), and Gomortegaceae, Siparunaceae, Atherospermataceae, and Monimiaceae of the core Laurales. The dissertation consists of three parts.

1 Floral phyllotaxis and floral architecture in Calycanthaceae (Laurales)

The present comparative studies show that floral phyllotaxis is uniformly spiral with a Fibonacci pattern in all four genera of Calycanthaceae. Although organs are initiated one after the other, they form series of the same kind in Fibonacci numbers (5, 8, 13, 21), regularly surrounding the floral centre. The extent of the transition zone from the vegetative decussate to the floral spiral phyllotaxis is linked to floral apex size and shape. Irregularities in organ sequence along the ontogenetic spiral occur at the transition between staminodes and carpels; the ratio of floral organ size to floral apex size is small during this phase, and organ identity appears to be determined by the neighboring organs rather than the position on the ontogenetic spiral.

Other new findings are the presence of food bodies on the anther tips and inner tepals, and of a valvate, saloon-door-like opening pattern of the thecae in *Sinocalycanthus*. The study also allowed reinterpretation of the morphology of fossil Calycanthaceae: all Calycanthaceous fossil flowers appear to be spiral (*Araripia*, *Virginianthus*, and even *Jerseyanthus*, which was originally described as whorled).

2 Comparative gynoecium structure and development in Calycanthaceae (Laurales).

Gynoecium structure was studied in a representative of all four genera of Calycanthaceae, and carpel development in a representative of each of the two subfamilies (Calycanthoideae and Idiospermoideae). Newly discovered shared features of both subfamilies include postgenital coherence between the free carpels with the formation of an extragynoecial compitum, abortion of the upper of the two ovules in preanthetic development, and lobation of the outer integument. Newly discovered differences include: carpel primordium shape, contribution of the outer integument to micropyle formation, and mode of formation of the extragynoecial compitum. Unexpectedly, at anthesis, ovary and ovules of *Idiospermum* are not larger than those of Calycanthoideae, despite the conspicuous difference in fruit (*Idiospermum* is unique in having the largest embryos of all angiosperms). Sterile carpel-like structures (carpellodes) are present only in *Idiospermum*.

The lateral ovule position in Calycanthaceae is correlated with a different development of carpel closure as compared to core Laurales, which exhibit median ovule position. In Calycanthaceae, the ovules are initiated at the lower portion of the carpel flanks, approximately concomitant with carpel closure; a cross zone is apparent only after carpel closure. In core Laurales, however, the ovuliferous cross zone is initiated earlier, long before carpel closure begins. In Calycanthaceae, the carpels close from the bottom upwards. In contrast, in core Laurales the large cross zone delays closure near the basis of the carpels, which proceeds from mid-length downwards.

3 Diversity and lability of floral phyllotaxis in the pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae)

Representatives of all families and most major subclades of pluricarpellate core Laurales were comparatively studied for the first time in order to solve contradictions and uncertainties in previous studies, and to find possible structural features linked with special types of phyllotaxis. In core Laurales, spiral, simple whorled, complex whorled, and irregular floral phyllotaxis patterns occur. Whorled and spiral phyllotaxis co-occur in all families, except Gomortegaceae. Floral phyllotaxis varies even within a species in some Mollinedioideae (Monimiaceae). Complex whorled floral phyllotaxis with two or more organs in a position where only one is expected and changes in merism are especially prominent in Atherospermataceae and Monimiaceae; complex whorls allow the transition from 2- to 4, 6- or 8-merous whorls. The presence, prominence, and diversity of complex whorls in flowers and their evolutionary significance are worked out here for the first time for two angiosperm families.

Small floral organ number is correlated with simple whorled patterns (2-merous whorls), and high organ number with complex whorled patterns. Pattern complexity is correlated with floral cup shape: flat, table-like floral cups allow initiation of the most complex patterns resulting in up to 8-merous whorls. Some species with the most complex patterns also have whorled flowers and spiral flowers in the same inflorescence; terminal flowers tend to have more organs and to be spiral, and lateral flowers tend to have fewer organs and to be whorled. In flowers with high organ number (>100 organs), irregular floral organ arrangement was found. Presence of a hyperstigma is correlated with double organ positions in the perianth. Irregularities in organ sequence were found at the periphery of the gynoecium in some Atherospermataceae and Monimiaceae, involving staminodes, carpellodes and carpels. In Laurales, floral phyllotaxis diversity appears to have evolved from spiral phyllotaxis, independently in Atherospermataceae, Siparunaceae, and Monimiaceae.

ZUSAMMENFASSUNG

Die vorliegende Doktorarbeit bringt neue Ergebnisse über die vergleichende Blütenstruktur bei phylogenetisch basalen Blütenpflanzen. Fünf Familien der Ordnung Laurales wurden in die Untersuchungen einbezogen: Calycanthaceae, die Schwestergruppe aller übrigen Laurales (core Laurales), sowie Gomortegaceae, Siparunaceae, Atherospermataceae und Monimiaceae der core Laurales. Die Dissertation besteht aus drei Teilen.

1 Blütenphyllotaxis und Blütenarchitektur bei Calycanthaceae (Laurales)

Die vorliegenden Untersuchungen zeigen, dass die Blütenphyllotaxis bei allen vier Gattungen der Calycanthaceae spiralig nach dem Fibonacci Muster ist. Gleichartige Blütenorgane bilden oft Serien mit Fibonacci Zahlen (3, 5, 8, 13, 21). Die Länge des Übergangs von der dekussierten vegetativen zur spiraligen Phyllotaxis der Blütenorgane hängt von der Grösse des Apikalmeristems ab. Unregelmässigkeiten in der Organsequenz kommen beim Übergang vom Androecium zum Gynoecium vor; das Verhältnis der Grösse der Organprimordien zur Grösse des Apikalmeristems ist während dieser Übergangsphase am kleinsten, so dass die Organidentität eher von den unmittelbar benachbarten Organen als von der Lage auf der ontogenetischen Spirale bestimmt zu werden scheint.

Neu für *Sinocalycanthus* sind Futterkörper auf der Konnektivspitze der Stamina und den inneren Tepalen, ebenso - neu für die rezenten Vertreter der Familie - ein valvates saloontürartiges Thekenöffnungsmuster. Die Arbeit ermöglichte auch, die Morphologie von fossilen Blüten der Calycanthaceae neu zu interpretieren: alle bekannten Blütenfossilien von Calycanthaceae scheinen spiralige Phyllotaxis zu haben (*Araripia*, *Virginianthus*, und auch der ursprünglich als wirtelig beschriebene *Jerseyanthus*).

2 Vergleichende Gynoeciumstruktur und -entwicklung bei Calycanthaceae (Laurales)

Die Gynoeciumstruktur wurde bei allen Gattungen der Calycanthaceae untersucht, und die Karpellentwicklung bei je einem Vertreter der beiden Unterfamilien (Calycanthoideae und Idiospermoideae). Neugefundene gemeinsame Eigenschaften der beiden Unterfamilien sind postgenitale Kohärenz der freien Fruchtblätter, die zu einem extragynoecialen Compitum führt, Abort der oberen der zwei Samenanlagen, und Lappenbildung an der Spitze des äusseren Integuments. Neugefundene Unterschiede sind: Form den Karpellprimordien, Beitrag des äusseren Integuments zur Micropyle und Art der Compitumbildung. Erstaunlicherweise sind zur Blütezeit die Ovarien und Samenanlagen von *Idiospermum* nicht grösser als jene der Calycanthoideae, obwohl die Samengrösse sehr verschieden ist (*Idiospermum* ist aussergewöhnlich, da es die grössten bekannten Embryonen aller Blütenpflanzen aufweist). Sterile karpellartige Organe (Karpellodien) kommen nur bei *Idiospermum* vor.

Die seitliche Stellung der Samenanlagen bei Calycanthaceae ist korreliert mit einer anderen Verschlussweise der Karpelle im Vergleich zu den core Laurales, die mediane Samenanlagen besitzen. Bei Calycanthaceae werden die Samenanlagen zuunterst an den Flanken der Karpelle angelegt, etwa gleichzeitig mit der Endphase des Schliessvorgangs; eine Querzone erscheint erst nach dem Verschluss der Karpelle. Bei core Laurales entsteht die Querzone früher, lange vor Beginn des Schliessvorgangs. Bei Calycanthaceae schliessen sich die Karpelle von unten nach oben. Bei core Laurales dagegen verzögert die grosse Querzone den Schliessvorgang an der Basis der Karpelle, der deshalb von der Mitte nach unten fortschreitet.

3 Diversität und Labilität der Blütenphyllotaxis bei den plurikarpellaten Familien der core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae)

Vertreter aller Familien und der meisten grösseren Subclades der plurikarpellaten core Laurales wurden untersucht, um das Ausmass der Diversität der Blütenphyllotaxis zu eruieren und Korrelationen zwischen den verschiedenen Phyllotaxismustern und anderen Blüteneigenschaften zu finden. In core Laurales kommen spiralige, einfache wirtelige, komplexe wirtelige und unregelmässige Phyllotaxismuster vor. Wirtelige und spiralige Phyllotaxismuster sind in allen Familien vorhanden ausser bei Gomortegaceae. Die Blütenphyllotaxis variiert sogar innerhalb einer Art bei gewissen Mollinedioideae (Monimiaceae). Komplexe wirtelige Phyllotaxis mit zwei oder mehr Organen anstelle eines einzigen und Wechsel der Zähligkeit sind besonders vertreten bei Atherospermataceae und Monimiaceae; komplexe wirtelige Phyllotaxis erlaubt Übergänge von 2-, bis 4-, 6-, oder 8-zähligen Wirteln. Das Vorkommen, die Häufigkeit und Diversität komplexer Wirtel in Blüten und ihre evolutive Bedeutung werden hier zum erstenmal für zwei Angiospermenfamilien herausgearbeitet.

Kleine Organzahlen sind korreliert mit einfacher wirteliger (dekussierter) Phyllotaxis und hohe Organzahlen mit komplexer wirteliger Phyllotaxis. Die Komplexität des Musters ist korreliert mit der Form des Blütenbechers: flache, tellerartige Blütenbecher erlauben die Bildung der komplexesten Muster, die zu bis zu 8-zähligen Wirteln führen können. Bei Arten mit den komplexesten Mustern kommen auch spiralige und wirtelige Blüten auf demselben Blütenstand vor: Endblüten tendieren dazu, mehr Organe und spiralige Phyllotaxis auszubilden, Seitenblüten dagegen weniger Organe und wirtelige Phyllotaxis. Blüten mit hoher Organzahl (>100) haben unregelmässige Phyllotaxis. Das Vorkommen eines Hyperstigmas ist korreliert mit

Doppelstellungen im Perianth. Unregelmässigkeiten in der Organsequenz zwischen Staminodien, Karpellodien und Karpellen wurden an der Peripherie des Gynoeciums bei gewissen Atherospermataceae und Monimiaceae gefunden.

Innerhalb der Laurales ist die Diversität in der Blütenphyllotaxis vermutlich unabhängig bei Atherospermataceae, Siparunaceae, und Monimiaceae aus spiraliger Phyllotaxis evoluiert.

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